The taphonomy of fallow deer (*Dama dama*) skeletons from Denmark and its bearing on the pre-Weichselian occupation of northern Europe by humans

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Abstract:

The ecological tolerances of Neandertals, their ability to subsist in the dense forests of full interglacials, and their capacity to colonize northern latitudes are the subject of ongoing debate. The site of Hollerup (northern Denmark) lies at the northern extreme of the Neandertal range. Dated by various techniques to the Eemian interglacial (MIS 5e), this site has yielded the remains of several purportedly butchered fallow deer (*Dama dama*). Taphonomic reanalysis of the remains from Hollerup and a handful of other Eemian-aged fallow deer skeletons cast doubt on the interpretation that they were humanly modified. We place this revised conclusion into the wider context of human settlement of southern Scandinavia during the Eemian. Other claims of Neandertal presence in the region rest on candidate Middle Paleolithic artifacts, all of which derive from surface contexts. With the fallow deer material removed as a secure indicator of Neandertal settlement of Denmark during the last interglacial, this lithic material must be viewed with renewed skepticism. While ecological and/or topographic factors may have played an important role in preventing Neandertals from penetrating into peninsular Scandinavia, we caution that geological, taphonomic, research-historical, and demographic factors may have significantly distorted our picture of their occupation in this region.

Keywords: Neandertals | Denmark | Scandinavia | Fallow deer | Hollerup | Colonization | Taphonomy

Article:

Introduction

The nature and timing of the human colonization of northern Europe (up to and beyond about 50° N) during the Pleistocene is a matter of debate (Roebroeks 2006; Hublin and

Roebroeks 2009; Hosfield 2011; Roebroeks et al. 2011). While this issue is critical for establishing the eco-cultural tolerances of Pleistocene human groups, explanations of *why* particular regions were colonized as they were depend heavily on what Roebroeks (2006, 425) calls "getting the pattern 'right'"; that is, the establishment of robust chronologies and reliable presence/absence data.

One of the more intriguing subplots in this debate surrounds Neandertal settlement of northern latitudes. Neandertals are generally considered to have been the first to establish a durable presence in a variety of northern temperate environments (Hublin and Roebroeks, 2009). Indeed, the Neandertal world has recently expanded, as DNA analyses suggest their presence as far east as Siberia (Krause et al. 2007), and the discovery of possible late Middle Paleolithic finds may place them just south of the Arctic Circle (Slimak et al. 2011, 2012; but see Zwyns et al. 2012). These new data and the debate over how Neandertal populations responded to environmental changes illustrate the difficulty of defining their range and how it fluctuated over time (van Andel and Davies 2003; Stewart 2005; Hublin and Roebroeks 2009; Dennell et al. 2011; Finlayson 2004).

One issue in particular that generated a great deal of discussion was Neandertals' ability to successfully handle fully interglacial, and arguably densely forested, European environments (e.g., Roebroeks et al. 1992; Gamble 1987). This question appears to have been settled, at least for the Eemian interglacial (corresponding to Marine Isotope Stage [MIS] 5e, ca. 127–115 kya [thousand years ago]; Brauer et al. 2007), as Neandertal presence in and adaptation to such habitats is attested at a small number of sites throughout the central and (to a lesser extent) western parts of northern Europe (Gaudzinski-Windheuser and Roebroeks 2011; see Fig. 3). It has even been argued that the general paucity of sites dating to MIS 5e reflects preservational biases rather than a true dearth of Neandertal settlement (Roebroeks and Speelers 2002). Recent research indicates that Neandertals in fact exploited a wide variety of environments during this time period, including rugged mid-altitude habitats (Daujeard et al. 2012) and coastal areas (Stringer et al. 2008; Hijma et al. 2012), the latter possibly as major colonization routes (Cohen et al. 2012). Nevertheless, Neandertals do appear to be absent in large parts of northern Europe during the Eemian, most notably Britain (Lewis et al. 2011).

This growing appreciation of Neandertal adaptability and colonization capabilities encourages a shift away from continent-wide, blanket explanations for presence/absence and towards more detailed, regionally specific scenarios that invoke factors beyond dichotomies such as forest versus steppe. Southern Scandinavia, and the area of present-day Denmark in particular, potentially offers unique insight in this context: the Jutland peninsula extends from just below 55° N at the modern German-Danish border to about 57.75° N at its present-day tip. It represents a natural extension of continental Europe and served as a colonization corridor for plants and animals alike throughout the Pleistocene (Aaris-Sørensen 2009; Donner 1995). Whether, and to what extent, humans participated in these events is less clear.

Claims that Scandinavia was occupied before the last (Weichselian, ca. 115–11.7 ka) glaciation have been made since the early twentieth century, most notably by Danish geologist Nicolaj Hartz (1909) and Swedish antiquarian Oscar Montelius (1921). Within a Victorian framework, the anthropologist Hans Peder Steensby (1908, 1911) suggested that modern humans descended

from “noble Neandertals” and that evidence for such an ancestry was found among contemporary Danish populations. This was embraced by Nobel laureate Johannes V. Jensen (1910) who considered, among others, the famous poet Hans Christian Andersen as an exemplar of this Neandertal heritage. Jensen was thus instrumental in popularizing and romanticizing the idea of a noble Scandinavian ancestry, which in turn had a lasting effect not only on the popular imagination but on scientific research within the growing field of Scandinavian prehistoric studies (Kjærgaard 2013).

While the earliest generally accepted dates for the human settlement of Scandinavia currently lay at the end of the Weichselian (Riede 2009; Brinch Petersen 2009; Mortensen et al. 2009), whether or not pre-modern humans ever ventured into the region remains contested. In fact, this issue has cultivated a rather lively (and sometimes acrimonious) exchange among both professional and amateur archaeologists about lithic material thought by some to be of Middle or even Lower Paleolithic manufacture and by others to be implements of Mesolithic or later age (Johansen and Stapert 1996). Debate on a pre-modern human settlement continues, with the contested hearth and modified pieces of wood from Laduholmen in Sweden (Heimdahl 2006) and purported Middle Paleolithic tools from Eemian-aged deposits at Susiluola Cave in Finland (Schultz 2002, 2007, 2010; Schultz et al. 2002; but see Pettitt and Niskanen, 2005) being the most recent cases. One common criticism of the Danish lithic material in particular is that none of the finds are associated with secure stratigraphic contexts and/or dates.

The site of Hollerup (56.40° N, 09.78° W) in northern Denmark is unique in that the evidence for a pre-modern human occupation comes not from lithics but from purportedly butchered animal bones that derive from a relatively well-dated stratigraphic context. In 1955, zoologist Ulrik Møhl-Hansen, then a conservator at the Zoologisk Museum (Statens Naturhistoriske Museum, Københavns Universitet) in Copenhagen, published a paper entitled *Første sikre spor af mennesker fra interglacialtid i Denmark: Marvspaltede knogler fra diatoméjorden ved Hollerup* or, in English, *The first definitive traces of Man from interglacial times in Denmark: Marrow-split bones from diatomite deposits at Hollerup*. In this paper, Møhl-Hansen contended that at least one, and perhaps several, fallow deer (*Dama dama*) skeletons recovered from Eemian-aged lake deposits at Hollerup had been broken open by humans for marrow. The study in fact originated as an osteological comparison of medieval fallow deer (which, having gone extinct in Demark, were reintroduced to the country during those times) with those from Hollerup. Before this comparison could be carried out, however, some of the long bones from Hollerup needed to be glued together. Møhl-Hansen concentrated first on a nearly complete female skeleton that he referred to informally as Find V (or Hollerup V)[1]. After refitting the long bone fragments, he noticed four things. First, the breaks on the bones appeared to be ancient and not the result of excavation or curation. This was considered odd, as Møhl-Hansen thought it unlikely that bones would be broken naturally after being deposited in a quiet lakebed. Second, some of the bone surfaces were flaked away around the areas where the breaks had apparently been initiated, which suggested that concentrated blows had been applied to those bones. The third observation was the remarkable symmetry in the way some bones from opposite sides of the animal had been broken (Fig. 1). Finally, Møhl-Hansen noted general similarities in the breakage patterns

[1] Møhl-Hansen (1955) referred to each fallow deer find analyzed in his study sequentially, based on the year of discovery, from I to XIV. Although this numbering system is followed here for the sake of comparison, the finds carry official catalog numbers in the Zoologisk Museum.

documented on the Find V skeleton relative to those seen on what he interpreted to be marrow-broken bones from Mesolithic and Neolithic sites as well as the refuse of recent Greenlandic hunters (Fig. 2). Although he was careful to note that no stone tool cutmarks were identified, it was finally concluded that only human behavior could explain the bone breakage and its symmetrical patterning and, therefore, Find V represented an animal whose long bones had been broken open by humans to access the marrow. Other fallow deer finds from Hollerup in addition to a handful from Ejstrup, Egtved, Raagelund, and Seest were then examined. Eventually, Møhl-Hansen then suggested that Find I, from Hollerup, was likely marrow fractured and, with less conviction, that Find III (Hollerup), Find VIII (Egtved), and Finds IX and XIV (both from Hollerup) may also have been exploited by humans. Given the inferred Eemian age of the Hollerup finds, he identified Neandertals as the likely culprit.

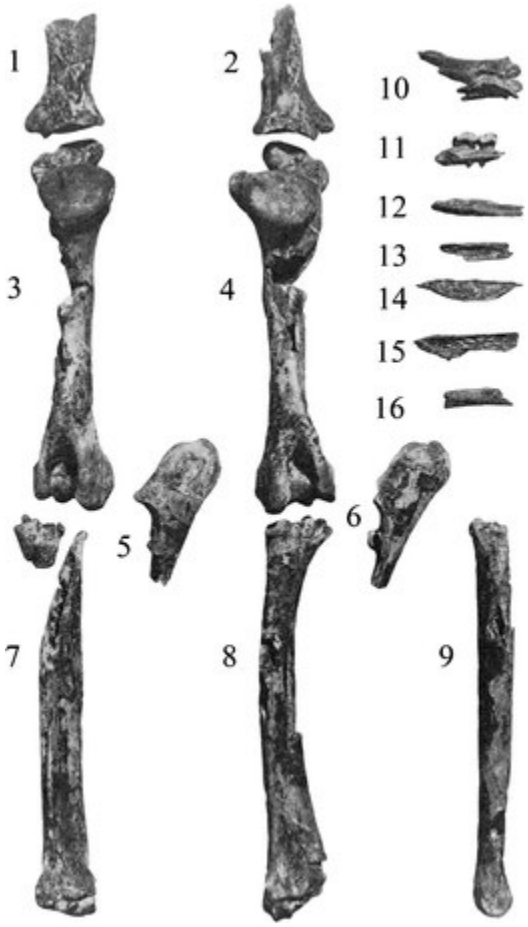

Fig. 1. Bones from Find V showing breakage patterns. *Numbers 3, 4, 8, and 9* were refit and glued together. One-third natural size. After Møhl-Hansen (1955, Fig. 2)

Fig. 2. Proximal radio-ulnae from Find V (*middle*) and from modern marrow-cracked reindeer from Greenland (*left*, *right*). Two-thirds natural size. After Møhl-Hansen (1955, Fig. 3a)

While one might question Møhl-Hansen's use of inferred, rather than known, marrow fractures as comparative samples, his analysis was significant for a number of reasons. First, with some notable exceptions (e.g., Pei 1938; Dart 1957), very few researchers at that time were analyzing bone breakage as a potential signature for early human behavior. Importantly, it was the first systematic presentation of data from a secure stratigraphic context to the question of Neandertal occupation in the region. As such, the study provided novel, well-reasoned, and stratigraphically controlled evidence for the first human presence not only in Denmark, but in all of northern Europe. It also temporarily reinvigorated research on the pre-modern human settlement of the region, as new claims were made and old ones resurrected in light of the allegedly secure evidence from Hollerup (Chapman and Chapman 1975, 42; Holm 1986, 76; Holm and Larsson 1995, 198–200; Becker 1971). In fact, several of the original Hollerup specimens are still on display at various museums throughout Denmark as evidence for a Neandertal presence in the country.

In 1992, an additional fallow deer individual was unearthed at Hollerup. The find, a ca. 3-month-old calf, was examined for butchery marks but no evidence for human intervention was detected (Björck et al. 2000, 523). The 1992 find also stimulated a reanalysis of the Find V material, with Björck et al. (2000, 524) concluding that no butchery marks or carnivore tooth marks were present, although they did leave open the possibility that humans had visited the site. As it stands then, contentions that the Hollerup material was exploited for marrow by Neandertals represent the earliest evidence (the hotly contested Laduholmen and Susiluola Cave evidence not withstanding) for human presence in the whole of Scandinavia. Here, we present a comprehensive taphonomic analysis of ten Pleistocene-aged fallow deer finds from Denmark, including several listed in Møhl-Hansen's (1955) original study, to determine if any were indeed butchered by humans. In doing so, this study (1) tests the broader hypothesis that humans were present in the region prior to the last Ice Age and (2) contributes to on-going debates of pre-modern human colonization capabilities, especially in regards to Neandertal settlement of interglacial forests and coastal habitats.

Materials and methods

Geological context and historical background

Hollerup is located between the modern towns of Ulstrup and Langå in north-central Jutland (Fig. 3). Commercial gravel and lime mining at the site in the late nineteenth and early twentieth centuries exposed thick sections of diatomaceous lake sediments (Fig. 4) where at least eight fallow deer finds were collected between 1897 and 1992 (Møhl-Hansen 1955; Hartz and Østrup 1899; Björck et al. 2000). While none of the remains were recovered through controlled excavations, their stratigraphic location was carefully recorded, which indicates that they all derive from a specific level within the 5 to 8.5-m-thick lacustrine deposits (Björck et al. 2000; Møhl-Hansen 1955; Hartz and Østrup 1899). The sediments are widely considered to be Eemian in age based on pollen and geological correlations (Björck et al. 2000; Kronborg et al. 1990; Andersen 1966; Jessen and Milthers 1928), being capped by Early Weichselian sands and Late Weichselian till and underlain by Saalian sands, gravels, and till (Fig. 5). Attempts to chronometrically date the lacustrine deposit via thermoluminescence produced dates between 77 and 88 kya (Kronborg and Mejdahl 1989), which, using a shallow trap correction (Mejdahl and Funder 1994), result in Eemian ages of ca. 120 kya. Uranium-series dates do not contradict this, although the ranges produced by the samples vary between 89 and 199 kya (Israelson et al. 1998). No stone tools have yet been reported from Hollerup.

Møhl-Hansen (1955, 102–104) lists fallow deer remains from four other locales: Ejstrup, Egtved, Seest, and Raagelund, the first three in south-central Jutland and the fourth on the island of Fyn (Figs. 3 and 5). Ejstrup is a gravel pit near the city of Kolding where two finds were made, one in 1900 (Find II) within "bog-like" sediment during the construction of train tracks, and the other (Find VII) in 1917 from a "freshwater gyttja". Find II was apparently a complete skeleton when originally uncovered, but only a handful of bones survived the tools of the workmen. The paperwork accompanying Find II in the Zoologisk Museum includes a short note by N. Hartz, in which he stated that "[t]he Ejstrup layer is certainly interglacial, full of fruits of *Carpinus* (hornbeam), which I have never found in postglacial layers in this country" (cited in Møhl-Hansen, 1955, 103). Pollen and geological correlations indicate that the peat and gyttja sediments at Ejstrup are Eemian in age (Houmark-Nielsen 1987, 37–39), and thermoluminescence samples from the peat deposit returned a date of 103 kya (Kronborg 1983, 244). One find, a nearly complete skeleton, was made near the village of Egtved in 1925, although this material could not be located in the museum. Three finds were made at Seest, a small suburb of Kolding, one in 1952 and two in 1954. Only the former, Find XI, was located in the museum collections. Little information is associated with this find other than reports of its recovery approximately 8 m below the surface (Møhl-Hansen, 1955, 104). The Raagelund find was made in 1936 at a gravel pit on the eastern outskirts of Odense, approximately 2 m below the surface in between a clay and gravel layer (Møhl-Hansen, 1955, 104). No stone tools have been identified at any of these sites.

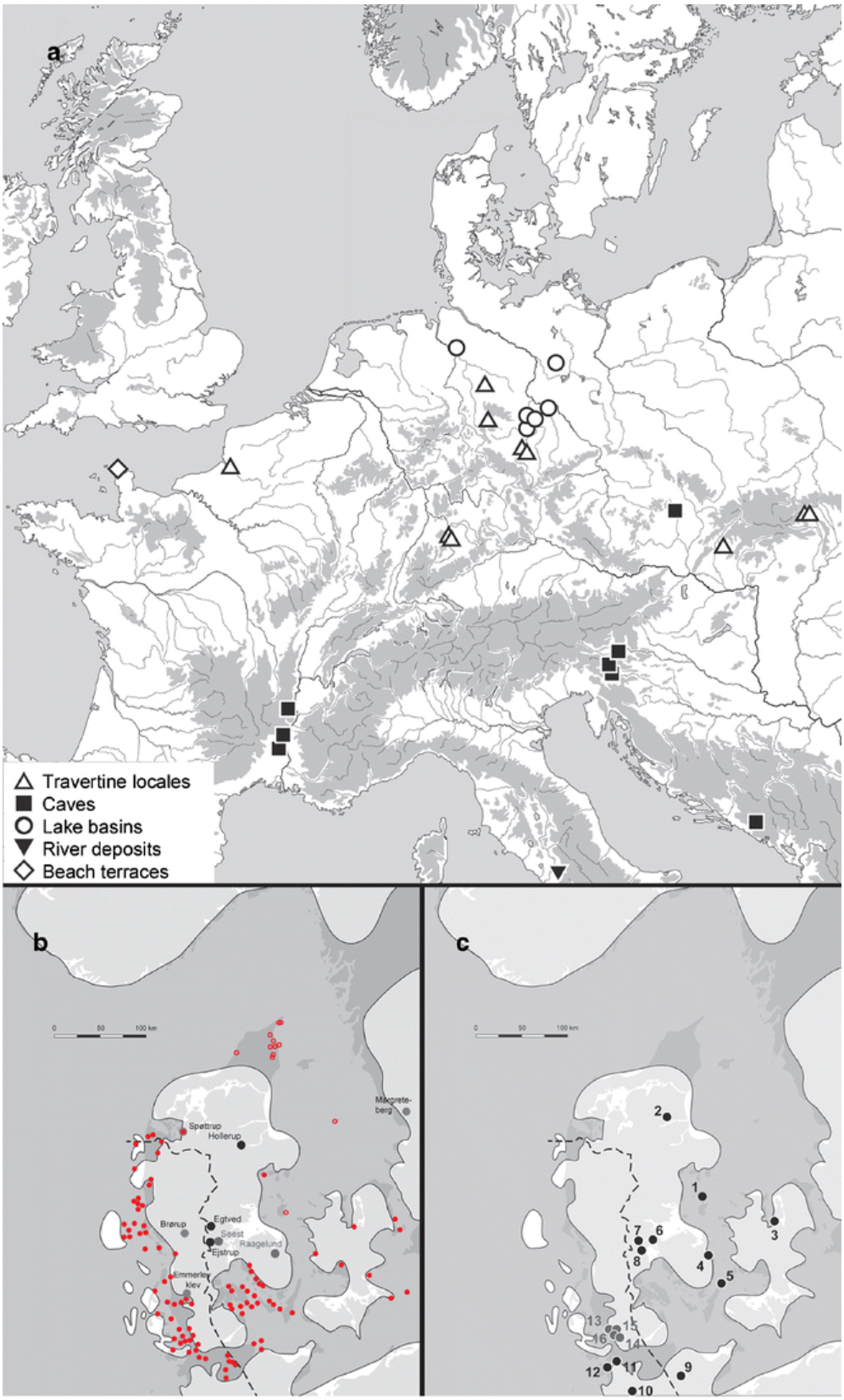

Fig. 3. a Map of Europe showing localities securely dated to MIS 5e (after Wenzel, 2007). **b** Map showing the location of Eemian-aged deposits in southern Scandinavia, including the fallow deer find sites mentioned in this

study (Hollerup, Egtved, Ejstrup, Seest, and Raagelund), other significant terrestrial deposits without fallow deer remains (Brørup, Emmerlev klev, Spøttrup, and Margreteberg), sites with marine deposits (*small circles*), and reconstructed MIS 5e coastlines relative to present-day conditions (after Larsen et al., 2009). The *dashed line* marks the maximum extent of the Weichselian glacial advance. Fallow deer finds from secure MIS 5e contexts are shown in *black*, finds from secondary/less secure contexts in *dark grey*. Eemian-aged geological locales with marine deposits are shown by *small circles* (*open* deep marine sediments; *closed* shallow marine sediments). **c** Map showing the locations of all candidate Middle Palaeolithic finds discussed by Hartz (1986) and Johansen and Stapert (1996). *1* Gammelholm; *2* Villestrup; *3* Ejby Klint; *4* Vejstrup Ådal; *5* Karskov Klint; *6* Fænø; *7* Seest; *8* Vejstrup Skov; *9* Kalübbe; *10* Oldendorf; *11* Schalkholz; *12* Hemmingsted; *13* Jägerhook; *14* Ahrenshöft; *15* Joldelund; *16* Drelsdorf. The cluster of finds in northwestern Germany just south of the Danish border (*13–16*, marked in *dark grey*) currently represents the northernmost verified Middle Palaeolithic artifacts in the study area as well as one of the northernmost Middle Palaeolithic locales in all of northwestern Europe. The age of this sizeable (<400 pieces) collection of lithics has been estimated to be Eemian (Hartz, 1986) or Early Weichselian (Hartz et al., 2012). Note the position of these finds to the west of the maximal extent of the Weichselian glacier, which contrasts with the distribution of candidate finds from Denmark

Fig. 4. Overview of the Hollerup site and close-up of sediments (*inset*). Much of the original profile has collapsed and been subsequently covered by slopewash and vegetation (compare with Björck et al., 2000, Fig. 3)

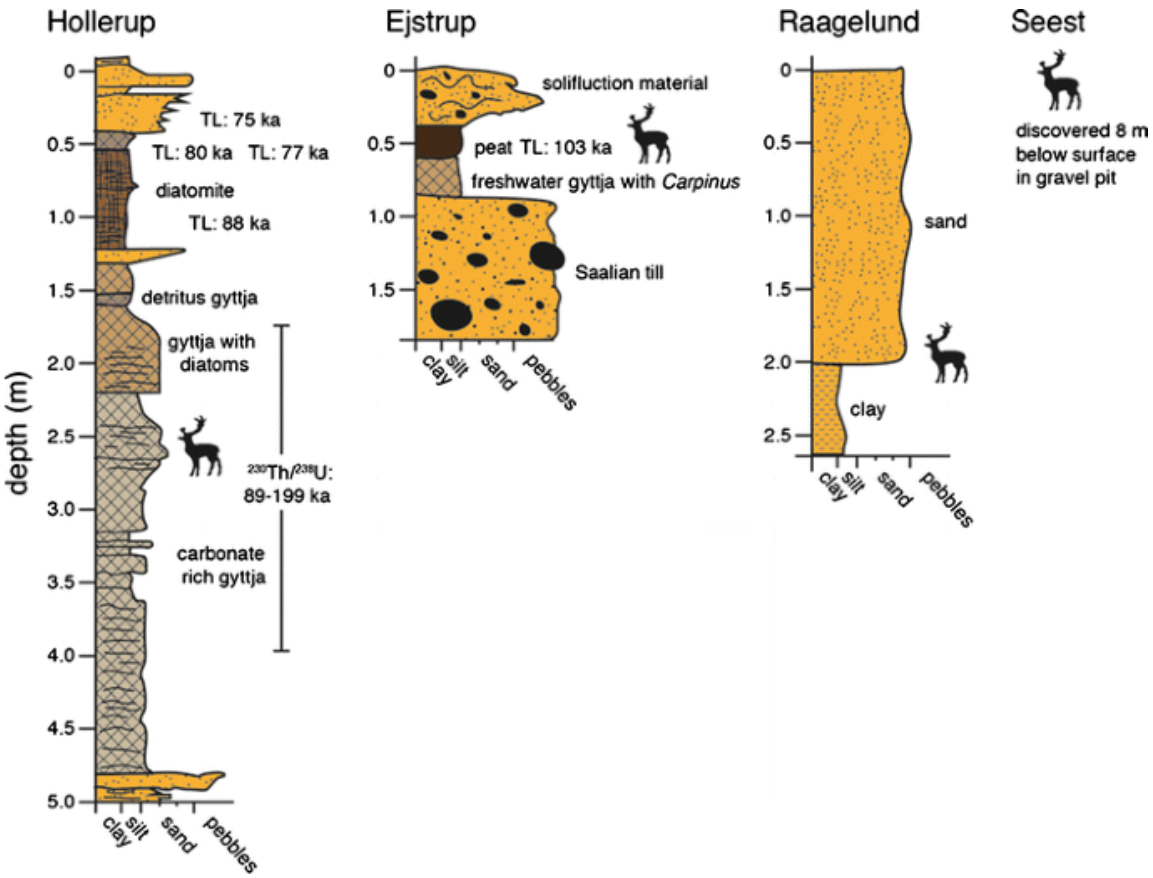

Fig. 5. Stratigraphic summary of fallow deer find sites. Data are from Houmark-Nielsen (1987), Israelson et al. (1998), Kronborg (1983), Kronborg and Mejdahl (1989), Mejdahl and Funder (1994), and Møhl-Hansen (1955)

Table 1. Summary of Danish fallow deer finds

Museum number	Find number	Site	Year of discovery
36.1897	**I**	**Hollerup**	**1897**
11.8.1900	**II**	**Ejstrup**	**1900**
??	III	Hollerup	1904
123.198	**IV**	**Hollerup**	**1906**
20.1.1913	**V**	**Hollerup**	**1912**
12.1915	**VI**	**Hollerup**	**1915**
122.198	**VII**	**Ejstrup**	**1917**
??	VIII	Egtved	1917
71.2011	**IX**	**Hollerup**	**1925**
7.1936	**X**	**Raagelund**	**1936**
17.1952	**XI**	**Seest**	**1952**
12.6.1954	XII	Seest	1954
??	XIII	Seest	1954
72.2011	**XIV**	**Hollerup**	**??**
73.2011	**XV**	**Hollerup**	**1992**

Finds in bold were located and included in the present analysis

Sample composition

Møhl-Hansen (1955, 102–104) listed a total of 14 fallow deer finds, seven from Hollerup (Finds I, III, IV, V, VI, IX, and XIV), two from Ejstrup (Finds II and VII), one from Egtved (Find VIII), one from Raagelund (Find X), and three from Seest (Finds XI, XII, and XIII). Of these 14, a total of ten (Finds I, II, IV, V, VI, VII, IX, X, XI, and XIV) were located in the Zoologisk Museum (where all the remains are currently housed) for analysis. The calf from Hollerup reported by Björck et al. (2000), referred to here as Find XV, was also included in the sample (Table 1), although the humerus listed in their report could not be located. Together, these 11 finds total 665 bone specimens.

Zooarchaeological and taphonomic variables

The maximum length of each specimen was measured with digital calipers (to the nearest millimeter) or an osteometric board (to the nearest centimeter). Four zooarchaeological measures of abundance are utilized in this study: number of identified specimens (NISP), minimum number of elements (MNE), minimum number of animal units (MAU), and minimum number of individuals (MNI) (see Lyman 1994). MNE estimates took into account the size, side, and ontogenetic age of each skeletally identifiable specimen, and a manual overlap approach (Bunn 1986) was used to derive element counts. All specimens were identified to species when possible and, following Brain (1974), to size class.

A systematic search for bone surface modifications was carried out on the faunas. All fragments were examined under a ×10–40 stereo microscope and a strong oblique light source (Blumenschine et al. 1996; Bunn 1981). Cutmarks, percussion marks, and carnivore tooth marks were identified following criteria outlined in Blumenschine et al. (1996, and references therein). Møhl-Hansen (1955, 119) was aware of cutmarks (*snitmærker*) and reported that none had been found on the Find V individual. He stated, however, that only the long bone ends of Find V were examined for cutmarks (because this is where they were typically found on the Mesolithic bones he examined), which implies that neither the remainder of the Find V skeleton nor the other finds were inspected for cutmarks. Møhl-Hansen (e.g., 1955, 110) also used the phrase "percussion marks" (*slagmæker*) in his study, but he was referring not to the microscopic pits and striations that are now known to be distinctive of hammerstone-assisted marrow fracturing (Blumenschine et al., 1996) but rather to macroscopic flaking and peeling around inferred impact points. In this analysis, four general categories of carnivore damage were recognized: (1) gnawing/furrowing, which involves sustained chewing of soft portions of bones and results in the partial or total destruction of those portions; (2) tooth pits, which are roughly circular in plan view and do not fully penetrate the thickness of the bone; (3) tooth scores, which are elongated (typically three or more times longer than they are wide); and (4) tooth punctures, which result when the bone collapses completely under the tooth and are characterized by distinct holes.

While morphological criteria are essential to the correct identification of surface modifications, the anatomical placement of the mark and the sedimentary context from which the specimen derives also offer critical information. Such a "configurational approach," where mark morphology and specimen context are taken into consideration, was practiced in this study (cf. Domínguez-Rodrigo et al. 2010). The location of surface modifications was recorded on digital templates in Adobe Photoshop and, further, were documented as occurring on the epiphyseal,

metaphyseal (near epiphysis), or diaphyseal (midshaft) sections of long bones (Bunn 2001; Domínguez-Rodrigo 1997). Subaerial weathering was recorded on all specimens for which it could be confidently scored following Behrensmeyer (1978) (Table 2), although analysis was limited to adult non-cranial specimens that are over 5 cm in maximum dimension. For each scored specimen, weathering was recorded first at the location displaying the maximum weathering stage and, second, on the anatomical aspect directly opposite the maximum weathering stage. Other surface modifications such as rounding, sediment abrasion, burning, and gastric etching were also noted (Shipman 1981; Behrensmeyer et al. 1986; Fiorillo 1989; Lyman 1994).

Table 2. Description of weathering stages used in the present analysis

Weathering stage	Description (cortical bone)	Description (compact bone)
1	Unweathered	Unweathered, articular surfaces intact with no surface cracking
2	Limited surface weathering; some longitudinal cracking	Articular surfaces intact with some surface cracking
3	Light surface flaking, deeper cracking	Articular surfaces exhibit some deterioration, but >50 % of articular surface remains intact
4	Patches of fibrous bone with moderate flaking and cracking	Intact articular surface restricted to a few small "islands;" <50 % of articular surface remains intact
5	Deep cracking and extensive surface flaking	No articular surface area remains intact

Descriptions from Behrensmeyer (1978) and Todd (1987)

Reliable interpretations of bone surface modifications require some sort of analytical control over cortical preservation, and five categories of surface degradation were recognized: (1) exfoliation, which includes, but is not limited to, subaerial weathering damage; (2) a manganese precipitate (Fig. 6) that manifests as a dentritic crust overlying the bone surfaces; (3) smoothing, which reflects the degree to which sharp-edged breaks or anatomical features are rounded and thus rendered less discernable; (4) dentritic etching, or the presence of shallow grooves oriented in a dentritic pattern (the same modification is referred to in many studies as "root etching"); and (5) pocking (Fig. 7), where areas of the cortical surface have been obscured by semicircular dents. These categories are meant to assess the relative fidelity of bone surfaces only and therefore do not necessarily imply the action of any specific taphonomic agent. Following Thompson's (2005) system, each modification type was scored for extent and severity. Extent reflects the amount of bone surface affected and was recorded in increments of 25 %: 0 (none of the bone surface covered), 25 (1–25 % covered), 50 (26–50 % covered), 75 (51–75 % covered), <100 (76–99 % covered), and 100 (entire surface covered). Severity measures the impact that each modification has on the bone surface and was scored subjectively from 0 to 3, with 0 reflecting no impact whatsoever (i.e., surface degradation is completely absent and, by necessity, extent also equals 0), and 3 a great impact that nearly obliterates the bone surface. Only "well preserved" specimens with nutritive phase breakage (see below) are included in surface modification calculations, where "well preserved" is defined as an extent of 25 or less, regardless of severity (a specimen with 25 % or less of its surface affected will likely preserve surface modifications regardless of how severely that small surface area is affected) or an extent of 50 or less and a severity of 0 or 1.

Fig. 6. Examples of low (*top*, thoracic fragment, 0–25 % coverage), moderate (*middle*, rib fragment, 25–50 % coverage), and high (*bottom*, scapula fragment, 75–99 % coverage) extent of surface coverage by magnanese precipitate on bones from Find V. All fragments exhibit a severity score of one, as the covering does not form a crust that would obsure surface marks. Photos by K. Hansen

Fig. 7. Proximal rib fragment from Find IV showing example of pocking (*arrows*). Photo by K. Hansen

Bone fragmentation was analyzed in several ways. The timing of fragmentation, either nutritive ("green" or "fresh") or non-nutritive ("dry"), was estimated based on the frequency occurrence of three fracture features (Villa and Mahieu 1991): fracture angle (the angle formed by the cortical and fracture surfaces), fracture outline (relative to the long axis of specimen), and texture of fracture surface. Nutritive breakage tends to create oblique (obtuse or acute) fracture angles, curved or V-shaped fracture outlines, and smooth release surfaces (Johnson 1985; Villa and Mahieu 1991; Morlan 1984). Only fractures occurring on diaphyseal sections were scored for these features. Because they have not been stained by the encasing sediments, recent breaks can typically be recognized by their distinct coloration. Those bones from Find V that had been glued

together (either during previous analyses or for museum displays) were separated to reveal the fracture surfaces by exposing the pieces to acetone fumes for approximately 24 h.

Specimens deriving from the six major long bones were coded following Bunn's (1982) system as preserving <50, >50, or 100 % of the original diaphyseal circumference. Marean et al. (2004, 82–85) show that experimental assemblages broken by humans and carnivores tend to be dominated by shaft fragments with less than 100 % of their circumference. They argue that the opposite pattern will be expressed when more identifiable (to element or taxon) long bone articular ends, which typically preserve sections of shaft that are complete in their circumference, are selectively collected and/or retained. This may reflect a more general bias, implying in turn that the assemblage is not representative of the taphoncoenose. Finally, a search for notches was carried out. Notches are arcuate features along the otherwise rectilinear outline of a fracture that result from nutritive phase breaching of long bone marrow cavities, usually by hammerstone-wielding humans or the dentitions of carnivores. Notches occur in a variety of forms, from complete features with two inflection points and non-overlapping flake scars to incomplete features that lack one or both inflection points due to breakage (Capaldo and Blumenschine 1994).

Osteometric measurements of the fallow deer remains follow the descriptions of von den Driesch (1976) and were recorded with digital calipers (to the nearest tenth of a millimeter) or an osteometric board (to the nearest centimeter). All measurements were taken three times, one day apart, and the average recorded. Paired element measurements from single individuals were averaged. Fallow deer dentitions were aged based on eruption schedules collated by Chapman and Chapman (1970) and molar wear codes defined by Brown and Chapman (1990). Wear codes are based on levels of dentine exposure on sloping enamel ridges, presence/absence of dentine linkages between cusps, presence of secondary dentine in the pulp cavity and, eventually, the eradication of infindibula. The most accurate and precise age estimates are derived from the combined wear scores of complete molar rows, although less precise estimates can be made based on isolated molars. The crown height of M_1s was measured from the highest point on the mesial-buccal cusp (the protoconid following the terminology of Brown and Chapman, 1990, 664) to the cemento-enamel junction following Moore et al. (1995).

Results

General assemblage composition

Table 3 summarizes the general assemblage composition of the fallow deer finds. Although not all material could be confidently identified to species, there is no reason to suspect that the specimens represent anything other than fallow deer. Each individual find represents an MNI of one. Find V is a more-or-less complete skeleton with only a handful of phalanges, ribs, and compact bones missing, while the remaining finds show a much more incomplete representation of elements (Table 4). Because of this, Find V is treated separately in many of the analyses that follow.

Table 3. General assemblage composition of the Danish assemblages by NISP

Find	*D. dama*	Mammal size 2	Mammal unidentified	Total
I (Hollerup)	4	0	0	4
II (Ejstrup)	7	0	0	7
IV (Hollerup)	55	21	0	76
V (Hollerup)	177	196	11	384
VI (Hollerup)	13	1	0	14
VII (Ejstrup)	24	0	0	24
IX (Hollerup)	7	0	0	7
X (Raagelund)	1	0	0	1
XI (Seest)	1	0	0	1
XIV (Hollerup)	1	0	0	1
XV (Hollerup)	144	2	0	146
Total	434	220	11	655

Table 4. Skeletal part representation for the Danish assemblages

	I (Hollerup)			II (Ejstrup)			IV (Hollerup)			V (Hollerup)			VI (Hollerup)			VII (Ejstrup)			IX (Hollerup)			X (Raagelund)			XI (Seest)			XIV (Hollerup)			XV (Hollerup)		
Element	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**	**NISP**	**MNE**	**MAU**
Cranium	1	1	1.0	3	1	1.0	22	1	1.0	34	1	1.0	1	1	1.0	4	1	1.0	0	0	0.0	1	1	1.0	0	0	0.0	0	0	0.0	18	1	1.0
Mandible	0	0	0.0	1	1	0.5	0	0	0.0	32	2	1.0	0	0	0.0	1	1	1.0	3	2	1.0	0	0	0.0	0	0	0.0	0	0	0.0	10	1	0.5
Hyoid	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Cervical vert.	0	0	0.0	1	1	0.14	12	7	1.0	41	7	1.0	1	1	0.14	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	4	3	0.43
Thoracic vert.	0	0	0.0	0	0	0.0	11	10	0.77	23	10	0.77	0	0	0.0	1	1	0.08	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	11	7	0.54
Lumbar vert.	0	0	0.0	0	0	0.0	0	0	0.0	8	3	0.6	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	13	5	1.0
Sacrum	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	2	1	1.0
Rib	0	0	0.0	0	0	0.0	25	10	0.38	67	9	0.35	1	1	0.04	16	9	0.35	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	2	1	0.04
Scapula	0	0	0.0	0	0	0.0	0	0	0.0	21	2	1.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Humerus	2	1	0.5	0	0	0.0	0	0	0.0	21	2	1.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Radio-ulna	1	1	0.5	1	1	0.5	0	0	0.0	8	2	1.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Carpal/tarsal	0	0	0.0	0	0	0.0	0	0	0.0	4	4	0.36	2	2	0.18	0	0	0.0	3	3	0.27	0	0	0.0	0	0	0.0	0	0	0.0	3	3	0.27
Metacarpal	0	0	0.0	1	1	0.5	1	1	1.0	6	2	1.0	3	2	1.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Innominate	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	4	2	1.0
Femur	0	0	0.0	0	0	0.0	0	0	0.0	2	1	0.5	2	1	0.5	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	8	2	1.0
Tibia	0	0	0.0	0	0	0.0	0	0	0.0	10	2	1.0	3	2	1.0	0	0	0.0	1	1	0.5	0	0	0.0	1	1	0.5	1	1	0.5	0	0	0.0
Metatarsal	0	0	0.0	0	0	0.0	0	0	0.0	5	2	1.0	1	1	0.5	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	4	2	1.0
Phalanx	0	0	0.0	0	0	0.0	0	0	0.0	7	7	0.29	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	3	3	0.13
Total	4	3	0.02	7	5	0.04	71	29	0.22	289	56	0.42	14	11	0.08	22	12	0.09	7	6	0.05	1	1	0.01	1	1	0.01	1	1	0.01	82	31	0.23

Carpal/tarsal includes lateral malleolus, calcaneous, and astragalus; cranium includes isolated teeth and antlers

Assemblage integrity and preservation

None of the fallow deer finds derive from systematic excavations. Most remains were unearthed during mining and/or construction operations and, once bone material was encountered, workers were often asked by an overseer to collect as many pieces as possible. In some cases, workers were even paid to salvage bones and were therefore motivated to do so as systematically as possible. As the assemblage of Find V from Hollerup (and presumably Find II from Ejstrup) shows, this collection strategy could result in the recovery of relatively complete skeletons and very small fragments. Nevertheless, the circumstances under which the fallow deer finds were brought to light certainly calls for an evaluation of how well they reflect what was originally present.

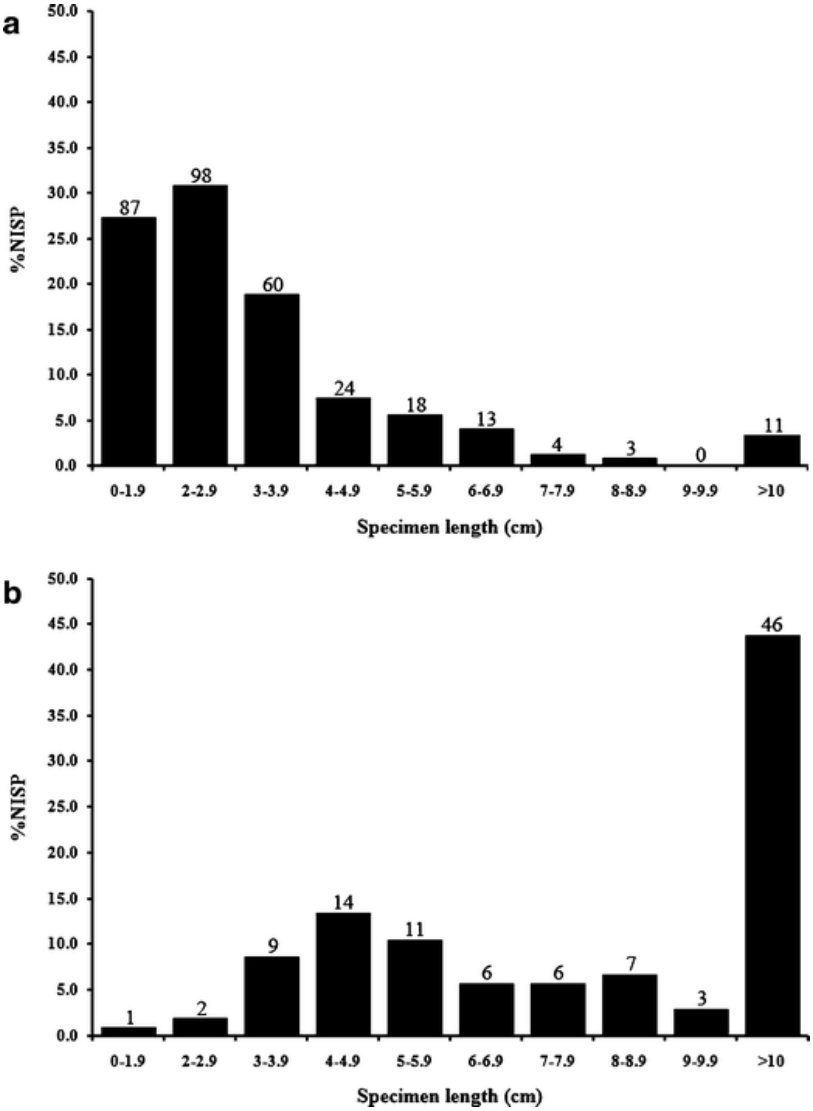

Fig. 8. Histogram showing frequency occurrence of fragment sizes for (**a**) Find V and (**b**) the other fallow deer finds combined. *Numbers atop bars* indicate raw counts. Counts exclude specimens with recent breakage

Table 5. Frequency occurrence of long bone shaft circumference types in the Danish assemblages and in an experimental assemblage of fresh-broken bones

	Find V		Other finds combined		Experimental	
Circumference type	NISP	%	NISP	%	NISP	%
<50 %	34	65.4	2	8.7	572	86.8
>50 %	5	9.6	0	0.0	45	6.8
100 %	13	25.0	21	91.3	42	6.4
Total	52	100.0	23	100.0	659	100.0

Experimental data from an assemblage of long bones broken by hammerstone and subsequently ravaged by hyenas. Hammerstone-only and carnivore-only experimental assemblages show nearly identical frequencies of circumference types (see Marean et al., 2004, Fig. 5)

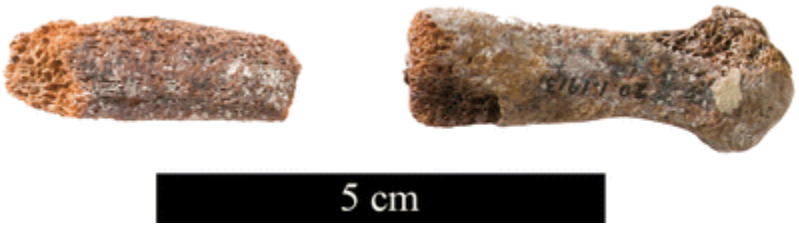

Fig. 9. Costal cartilage (*left*) and sternal element (*right*) from Find V. Photo by K. Hansen

Figure 8 demonstrates that the assemblages are clearly deficient in small specimens, which would be expected in a sample biased towards larger, more complete, and easier to notice fragments. The one exception to this is the Find V skeleton, which is represented by many small fragments. All of the assemblages except, again, Find V, are dominated by long bones preserving 100 % of their original diaphyseal circumference (Table 5). The preservation of the fallow deer remains from Hollerup is generally excellent, as even low-density elements like sternal and costal pieces (Fig. 9) and the epiphyses of the calf's long bones are preserved (see Björck et al., 2000, 523). The preservation of material from the other locales is more variable (Fig. 10). In terms of cortical surface preservation, a majority of specimens are affected to some extent by manganese precipitate, although most pieces show <50 % cortical coverage and low severity (Fig. 11). The only other factor affecting cortical surface preservation in the Find V assemblage is a single instance of smoothing (extent = 25; severity = 1) on a femoral shaft fragment. Smoothing ($n = 1$; extent = 25; severity = 1), dendritic etching ($n = 4$; extent = 25, severity = 1), exfoliation ($n = 2$; extent = 25; severity = 1), and pocking ($n = 1$; extent = 25; severity = 3) are relatively uncommon in the remaining assemblages.

Fig. 10. Lateral view of a left tibia from Find XI showing poor preservation. Photo by K. Hansen

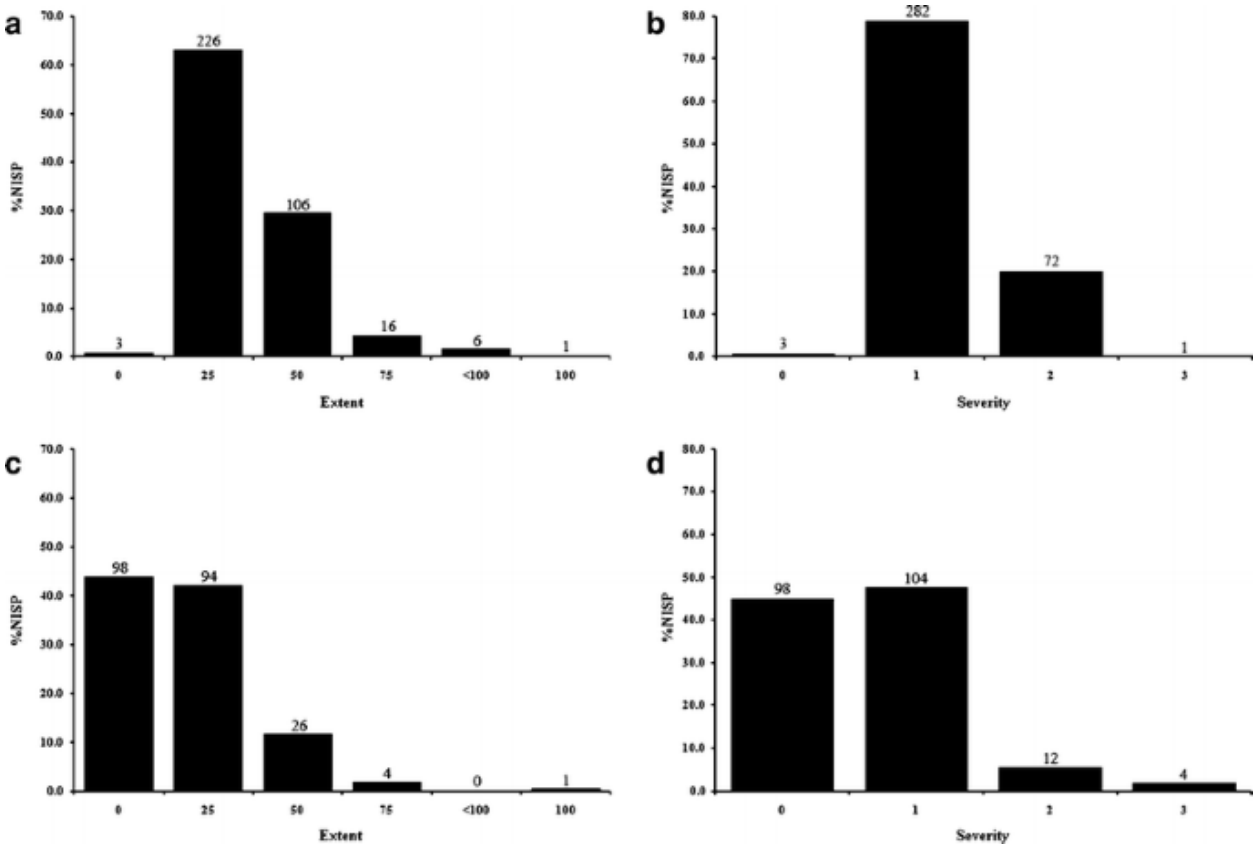

Fig. 11. Histograms showing frequency occurrence of extent and severity of manganese precipitate coverage for Find V (**a** and **b**) and the other fallow deer finds combined (**c** and **d**). *Numbers atop bars* indicate raw counts. Counts include all specimens regardless of breakage type

Bone surface modifications

A total of four marks, all of them from Find V, were identified as possible cutmarks or percussion marks. Mark 1 (Fig. 12), a series of striations on a rib fragment, is the most interesting and complicated. The individual grooves (labeled A, B, C, and D in Fig. 12) possess V-shaped cross-sections, although they lack the microstriations within their walls that are characteristic of stone tool cutmarks. Also unusual for true cutmarks are the shallow striations (marked by the arrow in Fig. 12) that abandon main groove B at an oblique angle. Finally, groove A and portions of grooves B and C display a coloration different from the surrounding cortical surface, which suggests that these marks, in whole or in part, were made subsequent to the specimen's removal from the sedimentary matrix, perhaps by an excavation or curation tool. It seems likely that multiple processes, acting at different times throughout the specimen's taphonomic history, were resposible for this set of marks. It is certainly possible, for example, that the excavation/curation damage partly obscured ancient marks. Groove B in particular could represent sediment abrasion (via trampling, for example), which is known to create marks simliar to groove B and the obliquely oriented striae that accompany it, although abrasion marks typically show a _/-shaped cross-section, a sinuous/curved trajectory, and microstriations within the main groove (Domínguez-Rodrigo et al. 2009), all of which are lacking in groove B. Sediment abrasion is also characterized by numerous shallow, randomly oriented striae (Behrensmeyer et al. 1986; Domínguez-Rodrigo et al. 2009), which, while recalling the shallow

striae attending groove B, are not seen elsewhere on the fragment nor on any other specimen in the Hollerup assemblages. The extremely fine-grained nature of the fossil-bearing horizon at Hollerup (Björck et al. 2000, 517–518) also argues against sediment abrasion as a significant factor. Stone tool butchery cannot be ruled out completely, but none of the marks can unambiguously be attribued to this activity. Mark 2 (Fig. 13) is made up of two pits. Pit A shows microstriations and associated crushing, both of which are typical of percussion marks. However, its presence on a rib fragment, which is not a regularly documented (though certainly not impossible) location for a percussion mark, that furthermore shows evidence of recent breakage leaves its identity in question. Microstriations are very atypical of tooth marks (Blumenschine et al. 1996, 496; Galán et al. 2009, 781), but given that nearby Pit B lacks microstriations, Mark 2 may represent a series of tooth marks. Mark 3 (Fig. 14) and Mark 4 (Fig. 15), located on fragments of a radius and tibia, respectively, are extremely shallow, smooth-walled dents that lack both the crushing and microstriations of percussion marks. It has been shown that unmodified hammerstones in particular can create percussion marks without microstriations, but even these generate pits with clear evidence of crushing (Galán et al. 2009). Nor can Marks 3 and 4 represent carnivore tooth marks, as tooth-on-bone contact too produces internal crushing (Blumenschine et al., 1996). In sum, none of the marks possess either the morphological or contextual features to confidently identify any of them as resulting from human butchery.

Fig. 12. Overview and close-up (*inset*) of linear striations on a rib fragment from Find V. See discussion of Mark 1 in text. Photo by M. MacNaughton

Fig. 13. Overview and close-up (*inset*) of a surface mark on a rib fragment from Find V. See discussion of Mark 2 in text. Photo by M. MacNaughton

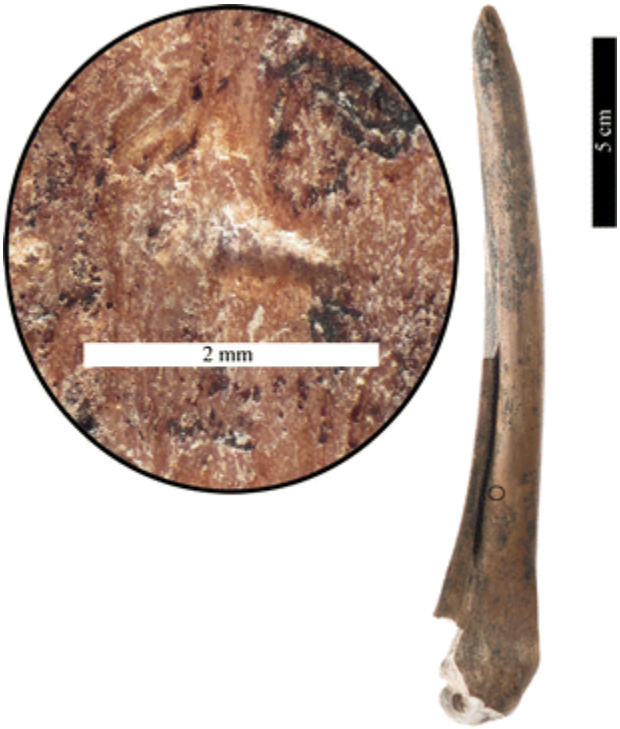

Fig. 14. Overview and close-up (*inset*) of a surface mark on a radius fragment from Find V. See discussion of Mark 3 in text. Photo by M. MacNaughton

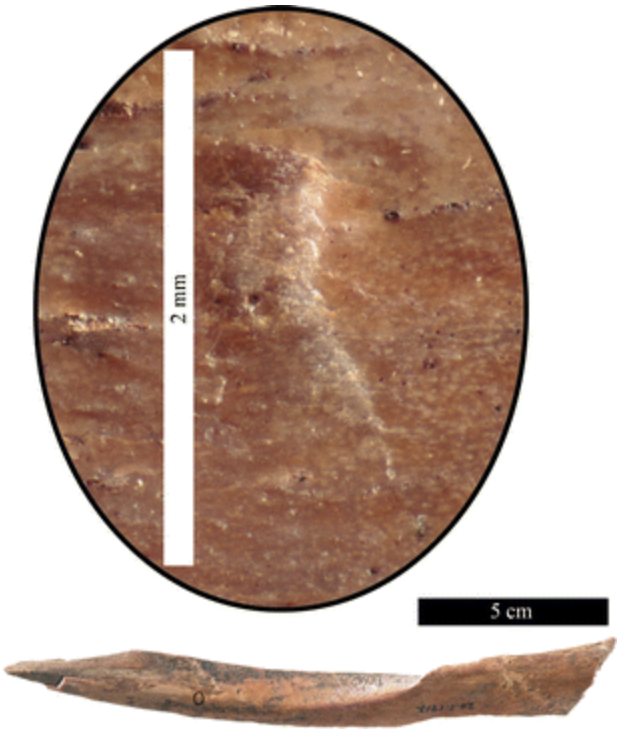

Fig. 15. Overview and close-up (*inset*) of a surface mark on a tibia fragment from Find V. See discussion of Mark 4 in text. Photo by M. MacNaughton

A total of nine specimens were found to bear carnivore tooth marks (Table 6 and Fig. 16), which includes the tooth-marked calcaneous from Find IX identified by Møhl-Hansen (1955, 117). Only four of the ten finds preserve evidence of tooth-marking. Regarding those four finds, and including only those specimens with good cortical preservation and nutritive breakage, tooth mark rates range from 9 to 67 % (Table 7). The weathering profile shows a preponderance of specimens that are unweathered or only slightly weathered (stage 1 or 2; Table 8 and Fig. 17). Two specimens, the femur fragment from Find V mentioned above and an antler fragment from Find X, show evidence for smoothing that may indicate fluvial abrasion (Andrews 1990; Shipman and Rose 1988). No evidence of burning was identified in any of the assemblages.

Table 6. Descriptions of tooth-marked fragments from the Danish assemblages

Find	Element	Tooth pits	No.	Location	Tooth scores	No.	Location	Gnawing	Location
I (Hollerup)	Humerus	Yes	9	Epiphysis	No	–	–	Yes	Proximal epiphysis
I (Hollerup)	Radius	No	–	–	Yes	1	Midshaft	No	–
IV (Hollerup)	1st rib, R	Yes	7	Blade	Yes	2	Blade	No	–
IV (Hollerup)	1st rib, L	Yes	6	Blade	No	–	–	No	–
IV (Hollerup)	Metacarpal	Yes	8	Proximal shaft	Yes	13	Midshaft	Yes	Proximal epiphysis
VII (Ejstrup)	Rib	Yes	1	Blade	No	–	–	No	–
IX (Hollerup)	Tibia	No	–	–	Yes	1	Midshaft	No	–
IX (Hollerup)	Calcaneous	Yes	>10	Shaft	Yes	>10	Shaft	Yes	Proximal epiphysis

R right, *L* left

Fig. 16. Medial view of right radius from Find I (**a**), caudal view of right humerus from Find I (**b**), and anterolateral view of right metacarpal from Find IV (**c**) showing tooth marks (*arrows*)

Table 7. Tooth mark frequencies in the Danish assemblages

Find	NISP TM	Total NISP	% TM
I (Hollerup)	2	3	66.7
IV (Hollerup)	4	27	14.8
VII (Ejstrup)	1	11	9.1
IX (Hollerup)	2	3	66.7
Total	9	44	20.5

Counts include only specimens with nutritive breakage and good cortical preservation (defined as an extent of 25 or less, regardless of severity, or an extent of 50 or less and a severity of 0 or 1)
TM tooth mark

Table 8. Frequency occurrence of maximum and flip-side weathering stages in the Danish assemblages

	Find V					
		Maximum weathering stage				
Flip-side weathering stage		1	2	3	4	5
	1	19	2	0	0	0
	2	–	10	0	0	0
	3	–	–	0	0	0
	4	–	–	–	0	0
	5	–	–	–	–	0
	Other finds combined					
		1	2	3	4	5
	1	21	5	1	0	1
	2	–	10	0	2	1
	3	–	–	4	0	0
	4	–	–	–	2	0
	5	–	–	–	–	0

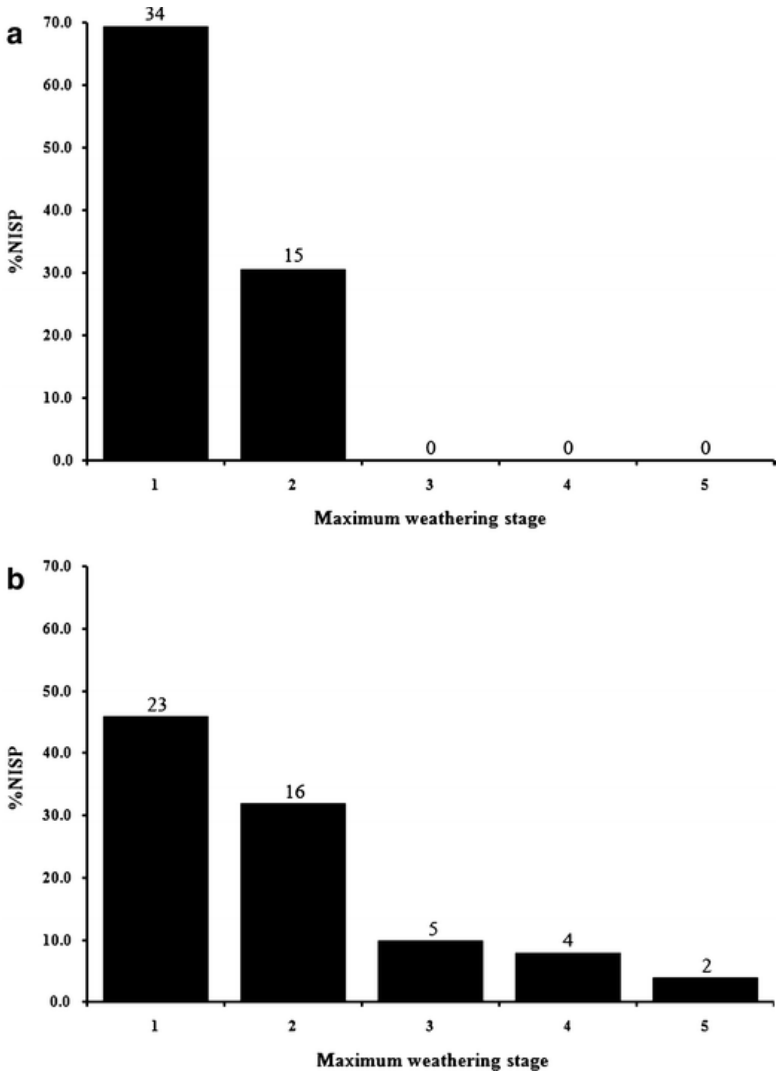

Fig. 17. Histograms showing frequency occurrence of weathering stages for Find V (**a**) and the other fallow deer finds combined (**b**). *Numbers atop bars* indicate raw counts. Counts exclude teeth, non-adult fragments, fragments <5 cm in maximum length, and fragments with recent breakage

Table 9. Frequency occurrence of fracture outlines and fracture angles in the Danish assemblages

	Find V		**Other finds combined**	
	NISP	**%**	**NISP**	**%**
Fracture outline				
Curved/V-shaped	30	41.7	3	17.7
Intermediate	12	16.7	3	17.7
Curved/transverse	10	13.9	5	29.4
Transverse	20	27.8	6	35.3
Total	72	100.0	17	100.0
Fracture angle				
Oblique	20	27.8	2	11.1
Oblique/right	23	31.9	5	27.8
Right	29	40.3	11	61.1
Total	72	100.0	18	100.0

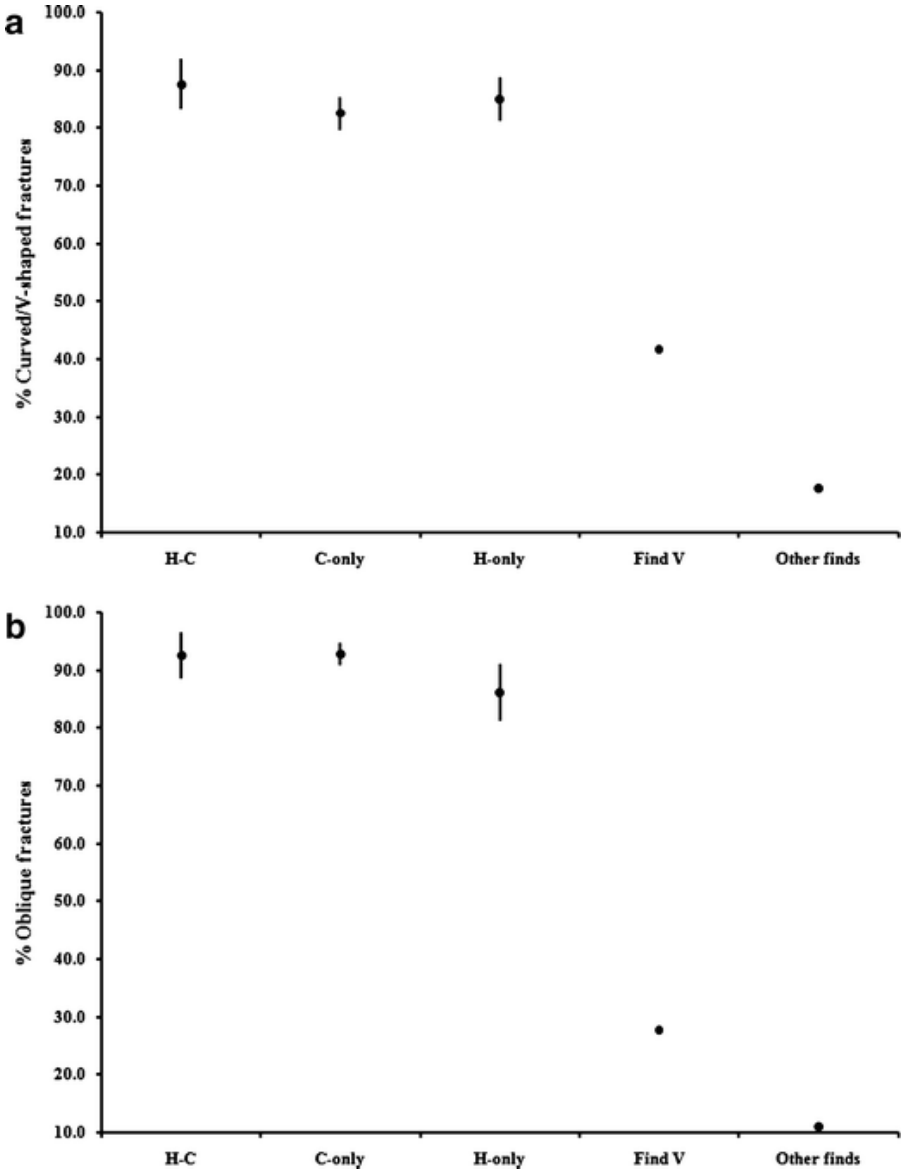

Fig. 18. Percentage of **a** curved/V-shaped fracture outlines and **b** oblique fracture angles for three experimental scenarios of fresh-broken long bones (*HC* human–carnivore, *C-only* carnivore only, *H-only* human only), Find V, and the other fallow deer finds combined. *Bars* indicate bootstrapped 95 % confidence intervals. Experimental data from Marean et al. (2000, Table 2)

Bone breakage

Table 9 summarizes the breakage data from Find V and the remaining assemblages. The frequencies of curved/V-shaped fracture outlines and oblique fracture angles on long bone fragments fall far below those produced in experimental assemblages of fresh-broken bones (Fig. 18), which suggests that non-nutritive breakage played a significant role in fragmenting the skeletons post-depositionally. Another way to identify post-depositional fragmentation is to examine the completeness of compact bones, which are rarely broken in a nutritive state (Marean 1991). Therefore, in the absence of butchery marks, tooth marks, or burning, any fragmentation of these bones is likely to have resulted from non-nutritive processes. A total of

four carpals and three tarsals are preserved in the Hollerup assemblages, and none show any evidence of nutritive phase modifications. Together, these specimens show a completeness index (see Marean, 1991) of 0.92, which suggests that some post-depositional fragmentation occurred. There are, nevertheless, indications that nutritive phase breakage did occur on some bones (Figs. 19 and 20). Post-fossilization and/or recent breakage was also documented, particularly on bones from Find V, as evidenced by the lack of sediment staining along the breakage surfaces (Fig. 20). Not a single notch, partial or complete, was identified among any of the skeletons.

Fig. 19. Cranial (*top*) and lateral (*bottom*) views of distal humeri from Find V. Both appear to show the smooth fracture release surfaces, oblique fracture outlines, and oblique fracture angles characteristic of nutritive phase breakage. Photo by K. Hansen

Fig. 20. Cortical (*top*) and medullary (*bottom*) views of a proximal tibia shaft fragment from Find V. The cortical view shows an example of the macroscopic flaking and peeling (*oval*) interpreted by Møhl-Hansen (1955) as an impact point. The medullary view shows a longitudinal breakage plane (*arrows*) that lacks the sediment staining of the surrounding surface, indicating that this particular fracture occurred well after the bones had been deposited and perhaps even after they had been removed from the matrix. Photos by K. Hansen

Osteometric measurements

Appendix I summarizes osteometric measurements for the fallow deer samples. Other than a single distal tibia from Seest (Find XI), all the measureable material derives from Hollerup. In addition to samples from modern *D. dama dama* (European fallow deer) and *Dama dama mesopotamica* (Middle Eastern fallow deer), comparative data are drawn from the following sites: Neumark-Nord 1 (Germany), which is an Eemian-aged lake dated to approximately 117 kya (Schüler 2010) with remains attributed to *Dama dama geiselana*; Swanscombe (England), where fossils referred to *Dama dama clactoniana* derive from Middle Pleistocene gravels thought to date to around 400 kya (Stringer and Hublin 1999); and Malpignano (Italy), a karstic cavity dating to the early stages of MIS 5 that also preserves the remains of *D. dama clactoniana* (Bologna et al. 1994).

The Find V cranial material is complete enough to demonstrate that it represents an adult female individual. Like other samples of Pleistocene European fallow deer, the Find V female falls above the range of variation of modern *D. dama dama* in most measures, and it lies at the low end of the sample of females from Neumark-Nord 1 (Fig. 21 and Table 10). Small sample size prevents a systematic comparison of multiple measures to determine the sex of the other Danish finds. However, given that Find V is known to be female and estimates of sexual dimorphism for Middle Pleistocene samples fall between 8 and 15 % (Pfeiffer 1999), it is likely that Find VI and Find XIV represent males. Antler fragments, while they cannot necessarily be assigned to the other skeletal elements with which they were found, are present in the Find I, II, IV, VI, VII, and X assemblages. Taken as a whole, the Danish material lies consistently within the range of variation seen at Malpignano (samples sizes at this site were not large enough to provide separate statistics for presumed males and females), while it appears either indistinguishable or smaller than the samples from Swanscombe (again, small sample sizes precluded a separate treatment of males and females) and Neumark-Nord 1 (Fig. 22 and Table 10).

Table 10. Results of single-sample *t* tests for osteometric differences between the Danish finds and modern and Pleistocene comparative samples

	***D. dama dama* (m)**	***D. dama dama* (f)**	***D. dama mesopotamica* (m)**	***D. dama mesopotamica* (f)**	**Neumark-Nord 1 (m)**	**Neumark-Nord 1 (f)**	**Swanscombe**	**Malpignano**
Scapula (GLP)								
Find V	−1.19	**3.26**	**−5.28**	−0.47	**−5.94**	–	**−2.78**	−0.45
Scapula (BG)								
Find V	**−2.65**	**3.82**	**−6.28**	0.57	**−4.07**	–	−1.82	−0.46
Scapula (LG)								
Find V	−1.00	**2.22**	**−7.32**	0.57	**−4.63**	–	**−3.14**	−0.68
Humerus (Bp)								
Find V	−1.51	**3.64**	**−4.80**	−0.44	**−6.63**	–	–	−1.57
Humerus (Bd)								
Find I	0.66	**3.51**	−1.36	0.57	**−2.20**	–	−0.90	0.42
Find V	−0.11	**2.54**	−1.85	−0.93	**−3.22**	–	−1.57	0.42
Radius (Bp)								
Find V	−0.39	**5.39**	**−3.81**	−0.22	**−4.47**	−1.62	–	−0.02
Metacarpal (Bp)								
Find V	**−2.09**	**2.23**	**−2.50**	**−2.06**	**−5.58**	−2.11	–	−0.87
Find VI	1.19	**6.29**	−0.72	**6.27**	**−2.18**	0.79	–	1.18
Metacarpal (Bd)								
Find V	−0.59	**4.02**	**−2.24**	−0.29	**−4.28**	**−2.05**	–	−0.43
Find VI	**3.32**	**8.58**	−0.09	**6.37**	−1.68	0.87	–	1.75
Tibia (Bd)								
Find V	−0.57	**2.71**	−1.80	−1.26	**−3.61**	−2.27	**−3.32**	–
Find VI	1.16	**5.26**	−0.66	**4.92**	−1.91	0.22	−1.12	–
Find IX	−1.57	1.23	**−2.45**	**−4.82**	**−4.60**	**−3.71**	**−4.59**	–
Find XI	1.04	**5.09**	−0.73	**4.50**	**−2.02**	0.05	−1.27	–
Find XIV	1.76	**6.14**	−0.27	**7.04**	−1.32	1.07	−0.36	–
Metatarsal (Bp)								
Find V	−0.99	**2.95**	−2.13	−2.05	**−3.37**	−2.02	−1.24	−0.29
Metatarsal (Bd)								
Find V	0.07	**4.72**	**−2.55**	1.27	**−5.60**	−2.01	−2.36	−0.93
Find VI	**3.32**	**9.34**	−0.16	**8.41**	−1.72	0.81	−0.71	**4.20**

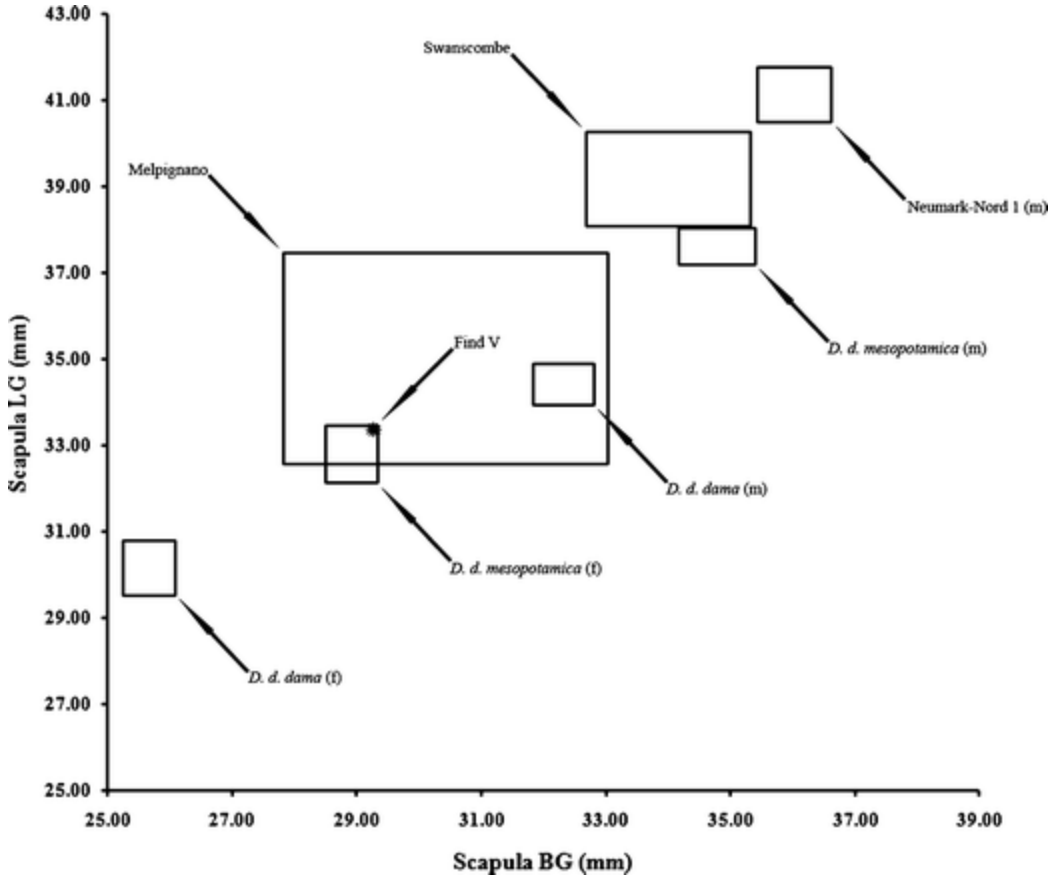

Fig. 21. Comparison of glenoid fossa measures for Find V and comparative fallow deer samples. *Boxes* represent 95 % confidence intervals. Comparative data from Pfeiffer (1999)

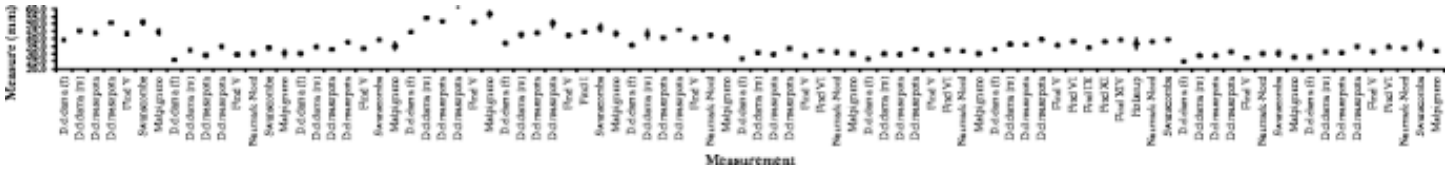

Fig. 22. Osteometric measures of Danish fallow deer compared to means and 95 % confidence intervals of osteometric measures for comparative fallow deer. Comparative data from Pfeiffer (1999)

Age determination

Two finds, Find V and Find IX, were complete enough to estimate age-at-death based on combined wear scores of complete molar rows. Molar rows in both individuals were fully erupted and showed relatively heavy wear. Using data from individuals of known age-at-death, Brown and Chapman (1990, 671) show that the association of age and combined wear score is best modeled by a curvilinear relationship. A multiple regression with age as the dependent variable was performed on Brown and Chapman's (1990, Table IV) raw data, which resulted in a significant relationship ($r^2 = 0.89$, $F = 132.13$, $p = 0.00$) described by the third-order polynomial equation:

$$\text{Age} = 6.925 + 0.121^{*}(\text{combinedwearscore}) + 0.008^{*}(\text{combinedwearscore})^2 - 0.0000194(\text{combinedwearscore})^3$$

The combined wear score of 81 for Find V (based on the right mandible) and 78 for Find IX (based on the left mandible) result in age estimates (with 95 % confidence intervals) of 61.47 ± 12.41 months (4.1–6.2 years) and 58.22 ± 12.31 months (3.8–5.9 years), respectively. Brown and Chapman's (1990) study includes only a handful of older adults (there are three individuals over the age of five) so, all else being equal, this sample will probably underestimate the true ages of older individuals. Brown and Chapman (1990, 679) in fact note that older animals tend be aged less accurately than younger animals, which probably reflects the accumulation of stochastic intra- and inter-individual variation with age. The third-order polynomial estimate of Moore et al. (1995, 31), which is based on a separate set of known age individuals that includes a more even distribution of ages (males and females combined), produces an estimate of 110.01 months (9.16 years) for Find V and 98.86 months (8.23 years) for Find IX[2]. Molar rows for the Find II and Find VII dentitions were not complete enough to calculate combined wear scores, although the M_3 is erupted and fully functional in both individuals which, based on modern proxies, indicates an age of at least 2.5 years (Chapman and Chapman 1970, 1975). Find II and Find VII are likely younger than both Find V and Find IX, as the former show higher crown heights and less severe wear on those molars for which it could be scored. The right mandible of Find XV shows fully erupted and in-wear deciduous premolars and a partially erupted M_1. Björck et al. (2000, 517) provide an age estimate of 2–4 months, which is entirely consistent with comparisons of known age individuals from the Zoologisk Museum collections.

Because the wear scores strictly apply only to animals living under conditions similar to those of the individuals from which the original data were collected, they should not be treated as absolute, single point ages but rather as relative estimates to aid assignments into broad age categories (juvenile, prime, and old) based on breeding capability and maximum potential lifespan. Most researchers consider the transition from "prime-aged" to "old" to be between about 50 and 70 % of maximum lifespan (Steele 2005, 414). Life expectancy in modern enclosed populations of unprovisioned European fallow deer is around 9–13 years (although females as old as 22 years have been recorded; McElligott and Hayden 2000) and male reproductive probability declines rapidly after age nine (McElligott et al. 2002). Therefore Finds V and IX are best characterized as old adults, while Finds II and VII likely represent prime-aged individuals.

Taphonomic history of the fallow deer assemblages

We explore the formational histories of these assemblages in three phases (Capaldo 1997; Marean et al. 2000; Blumenschine 1986; Gifford 1981). The first, referred to as the "recovery phase," reflects how recovery and curation protocols influence the sampling of an assemblage. The second is the "non-nutritive phase," which documents processes that effect bones in ways unrelated to the extraction of nutrients (e.g., weathering or trampling). Finally, the "nutritive phase" involves agents, most notably humans and carnivores, which process carcasses for nutrition. While in theory these phases are distinct in timing, signature, and/or effect, the latter two in particular commonly overlap.

[2] The regression equation of Moore et al. (1995) was constructed with wear scores of both mandibles combined. For Find V, the right M_1 could not be scored but was assumed to have the same wear score as the left M_1; likewise, for Find IX, the left M_2 could not be scored but was assumed to have the same wear score as the right M_2.

Recovery phase taphonomic history

Overall, it appears very likely, with the possible exception of Find V, that the fallow deer assemblages do not fully reflect what was originally present in the sediments at the time of their recovery. These assemblages are probably biased towards larger, more complete, and more easily recognized skeletal material. It is therefore possible that the missing parts of the assemblages included specimens with nutritive phase modifications (cutmarks, percussion marks, burning, percussion notches, percussion flakes, and carnivore tooth marks). Short of opening up new, systematic excavations at the sites, this point is impossible to address with any certainty. It can be said, however, that larger (and thus more likely to be collected) fragments, because of their increased surface area, tend to preserve at least surface marks at higher rates than do smaller (and thus less likely to be collected) fragments (Faith 2007). Some of the breakage observed in the assemblages occurred during the recovery phase, most likely during the extraction of specimens from the sediments.

Non-nutritive phase taphonomic history

Processes acting in the non-nutritive phase were the main agent (or agents) of breakage. Weathering is known to weaken bones and can thus cause pre-burial fragmentation or make bones more susceptible to pre- and post-burial breakage by other processes. Given the low overall levels of weathering in the assemblages, however, this is an unlikely agent of breakage. In their analysis of the Find XV calf, Björck et al. (2000, 523) suggested that "breakage was most likely caused by sediment compaction and loading." Sediment compaction and perhaps gelifraction, coupled with the leaching of organic material during burial, seems a reasonable explanation for the non-nutritive breakage in the assemblages, although there is very little experimental work in this arena (Guadelli 2008; Marean 1991). Weathering profiles demonstrate that the assemblages were not exposed subaerially for an extended period of time, and there is no evidence to suggest that fluvial processes transported the assemblages any great distance.

Nutritive phase taphonomic history

No definitive evidence of butchery was identified on any of the fallow deer skeletons, either through bone breakage or surface modifications. One point that is made nicely by the ambiguity of Mark 1 on Find V (Fig. 12) is how difficult it can be to interpret *individual* marks even with well established criteria for particular mark *classes* (e.g., cutmarks, tooth marks, etc.). The problem here is that diagnostic criteria for particular classes of marks are generalizations based on dozens or even hundreds of marks. Just as any one mark within a comparative sample of known derivation may not possess all the typical features of that particular class of marks, so too may an isolated mark of unknown origin. Compounding this is the likelihood that multiple processes were responsible for the various grooves of Mark 1. Nevertheless, while stone-tool-assisted butchery cannot be totally ruled out as the source of some of the marks on the Find V skeleton, the bulk of the morphological and contextual evidence argues against it.

Several other issues need to be considered before the question of human involvement is closed. First, poor preservation can make surface modifications difficult or even impossible to identify

(Thompson, 2005). Although the cortical preservation of the finds is generally excellent, patches of bone surfaces, particularly on the Find V individual, are covered by a manganese precipitate that could potentially obscure butchery marks. As we have seen, however, most specimens are only sparsely covered and the precipitate rarely forms a crust thick enough to totally obscure marks. So, if any butchery marks were present on the skeletons, it is likely that at least one convincing example would have been identified. Nonetheless, the presence of concealed butchery marks cannot be ruled out. The identification of percussion notches, on the other hand, is not affected by surface coverage (at least the extent seen among these assemblages), although they do tend to occur in relatively low frequencies regardless, even among experimentally broken assemblages (Pickering and Egeland 2006). Second, it has been demonstrated that selective collection and/or retention affected all the assemblages, which means that the missing fragments may possess butchery marks. The final issue concerns Neandertal butchery strategies. The lack of cutmarks was interpreted by Møhl-Hansen (1955, 119) as evidence that Neandertals did not use stone knives to cut meat from the bones, and the slight differences in breakage patterns between Find V and later time periods were thought to reflect a more "primitive" method of bone breaking. Rather than initiating several blows along the length of a long bone as seen among the Mesolithic and Neolithic material illustrated by Møhl-Hansen, the Neandertals at Hollerup apparently utilized a single blow to expose the marrow cavity and, in some cases, used their hands to manually fracture bones without the aid of hammerstones. This also could have been accomplished by striking a disarticulated long bone like a club against a hard surface, a technique that may not produce percussion notches (Noe-Nygaard 1977, 230–231; no mention is made about whether such a process creates percussion marks, but this presumably would depend on the amount of adhering soft tissue and the composition of the impacted surface). While such arguments could potentially explain the lack of butchery marks on the remains, this scenario runs counter to more recent research, which indicates that when Mid- to Late Pleistocene Eurasian Neandertals butchered medium-sized prey they produced bone refuse with numerous cutmarks, percussion marks, and percussion notches (Blasco and Fernández Peris 2012; Gaudzinski 2004; Marean and Kim 1998; Miracle 2005; Valensi 2000; Valensi et al. 2012; Niven et al. 2012). It is, of course, possible that a combination of small sample sizes and selective retention (as argued above) has artificially eliminated any such definitive evidence for butchery in the Danish assemblages.

There does appear to have been a small amount of nutritive phase breakage. For those specimens with tooth marks such breakage can be explained by carnivore activity. In the absence of clear-cut butchery or carnivore damage, nutritive breakage is more difficult to account for with Find V. Given the preponderance of non-nutritive breakage on the skeleton, it is possible that the other breakage, while appearing nutritive, actually took place well after the animal died and was in fact not associated with nutrient removal. It is known that the ambient environment is critical in determining how long a bone will retain "green" fracture characteristics when broken. Karr and Outram (2012), for example, found that experimentally frozen (−20 °C) bones can retain some green fracture features for 60 days, while bones subjected to an artificial hot and dry (40 °C) environment degrade very quickly and show very few green features after only 1 day. In a study of bones fractured via non-nutritive processes in temperate environments, Haynes (1983, 111) observed that "spirally fractured long bones have been found in open and dry grassland, but they are more numerous in well-shaded and moist areas such as woods, parkland, and thick grass sedge meadows, or in wet areas such as pond and lake bottoms or stream crossings, where the

deteriorating effects on bones of ex vivo weathering are considerably reduced, and where there is heavy bison traffic. Bones in the latter areas eventually disappear into the mud due to continued trampling. Many fractured bones possess a spiral fracture edge offset by a linear section of fracture edge, thus exhibiting attributes of two kinds of breakage." This observation mirrors very closely the situation seen at Hollerup (a lake environment) and on the Find V skeleton in particular (a mixture of breakage types).

Summary

It seems that the fallow deer carcasses experienced little or no modification by nutritive phase agents and, in cases where they did, it was carnivores that were responsible. Coincidently, the tooth-marked bones provide the only definitive evidence of carnivores' presence in Denmark during the Eemian, as their fossils are absent in deposits of that age (Aaris-Sørensen et al. 1990). Although the size of tooth marks has been shown to reflect at least the size of the carnivore responsible (Domínguez-Rodrigo and Piqueras 2003), the sample size of measureable marks from the fallow deer assemblages is simply too small to be meaningful. For the one find that appears to have been collected in its entirety (Find V), the vertebrae and long bone epiphyses are largely intact. The Find XV calf also preserves several vertebrae and unfused epiphyses. These portions, because of their low structural density and nutritional value, are regularly deleted by carnivores (Pickering et al. 2003), and a 3-month-old calf could easily be devoured completely by a medium- to large-sized carnivore (Pobiner and Blumenschine 2003; Stiner et al. 2012). This suggests that in the vicinity of the Hollerup paleolake (1) carnivore density was low and herbivore density high, the result being less intense competition and thus lower levels of carcass destruction (Faith and Behrensmeyer 2006; Faith et al. 2007; Selva et al. 2003) and/or (2) the carcasses were largely unavailable to carnivores. Perhaps, as Björck et al. (2000, 531) speculate for Find XV, these animals drowned well out in the lake while walking on weak ice. This is certainly possible, as the calf's age and a June–July birth (Chapman and Chapman 1975) point to an August–December death. None of the antler fragments from Hollerup are naturally shed, which indicates mortality for those individuals between September and April.

What is interesting about the Hollerup paleolake in particular is the presence of at least eight fallow deer (currently representing the northernmost occurrence of the species in the Pleistocene; Pfeiffer 1995), all from the same stratigraphic layer. Low levels of weathering and a lack of smoothing indicate that most of the individuals were not exposed for an extended period of time and were deposited near where they died. It is known that lakes are hotspots of biological activity and, relative to the surrounding landscape, bones tend to accumulate at higher rates around water sources via drowning, predation, and drought (Behrensmeyer 1987; Haynes 1988; Hutson 2012; Capaldo and Peters 1995). It therefore seems that Hollerup, and the other Eemian lakes throughout Denmark where faunal material is preserved, naturally attracted herbivores and carnivores and thus proved to be particularly favorable to the natural accumulation of bone.

Eemian lakes elsewhere in Europe also appear to have played a similar role as magnets for bone accumulation. For example, at Neumark-Nord 1 in Germany, which is one of a complex of sites scattered over hundreds of square meters within two Eemian-aged lake basins, the skeletons of over 100 fallow deer (in addition to several other species), many of which were more-or-less complete, were recovered from lacustrine sediments (Mania et al. 1990). Several individuals

show dorsal flexion of the head and neck, which results from perimortem overcontraction of the dorsal muscles following a central nervous system insult (e.g., hypoxia) just before death (Faux and Padian 2007). The retention of such a position strongly suggests in situ deposition with little or no influence by other taphonomic agents prior to burial (Gaudzinski 2004). On the other hand, stone tools were recovered from the lake margin and there is evidence in the form of definitive cutmarks that at least some of the deer carcasses were processed by humans. While it has been suggested that the deer were intentionally herded into the lake by Neandertals, others interpret the remains as natural deaths, perhaps the result of toxic bacterial blooms (Braun and Pfeiffer 2002). Regardless of how the carcasses were deposited (see Kindler et al. 2010; Mania 2010; Meller 2010 for recent work at Neumark-Nord), it seems that the paleolake at Neumark-Nord, like that at Hollerup, drew biological activity and thus promoted the deposition of bones.

Neandertals in Scandinavia and the colonization of northern latitudes

Prior to Møhl-Hansen's study, a number of flakes as well as chopper- and handaxe-like artifacts recovered throughout Scandinavia were considered to be Middle or even Lower Paleolithic implements (Højrup 1947; Bjørn 1928; Mathiassen 1935; Berthelsen 1944; see Fig. 3). Their surface context, however, ensured that these claims received little serious attention. What made the Hollerup evidence so intriguing was its secure stratigraphic context. In fact, Møhl-Hansen's publication created something of a sensation that eventually found its way into Denmark's museums. Additional claims of pre-modern human lithic material followed on the heels of the Hollerup study (see Johansen and Stapert, 1996 for a critical review of this evidence) but, again, none of these finds could be fixed stratigraphically. Similar interpretations of what were often heavily rolled specimens from northern Germany were met with harsh criticism (Prufer 1956; Hachmann 1974), and many candidate lithics from that region have since been discounted (Baales et al. 2000; Schwabedissen 1970).

Glacial deposits in southern Scandinavia are extremely rich in flint, which makes it difficult at times to distinguish geofacts from artifacts (Petersen 2008). To complicate matters further, choppers and rough handaxe-like implements were used to open oysters during the Mesolithic, and late Neolithic/early Bronze Age bifacial preforms can easily be confused with handaxes (Schwabedissen 1968; Troels-Smith 1995) (see Fig. 23). Some have gone as far as to suggest that most if not all Scandinavian handaxes are in fact such preforms, referring to these pieces as "archaeology's flying saucers" (Glob 1963) and "dangerous flints" (Glob 1972, 18). The application of microscopy-based methodologies cast further doubt on the age of most of the candidate lithics although, somewhat ironically, the handaxe-like implement referred to by Glob (1963, 1972) as a definitive example of a later prehistoric preform did stand out as possibly Middle Paleolithic in age (Johansen and Stapert, 1996). While genuine Middle Pleistocene-aged lithic material is known from nearby northern Germany (Hartz 1986; Hartz and Fiedler 1997; Hartz et al. 2012), these too have been interpreted in reference to the evidence from Hollerup. Genuine or not, none of the candidate lithics from within Denmark are associated with secure dates.

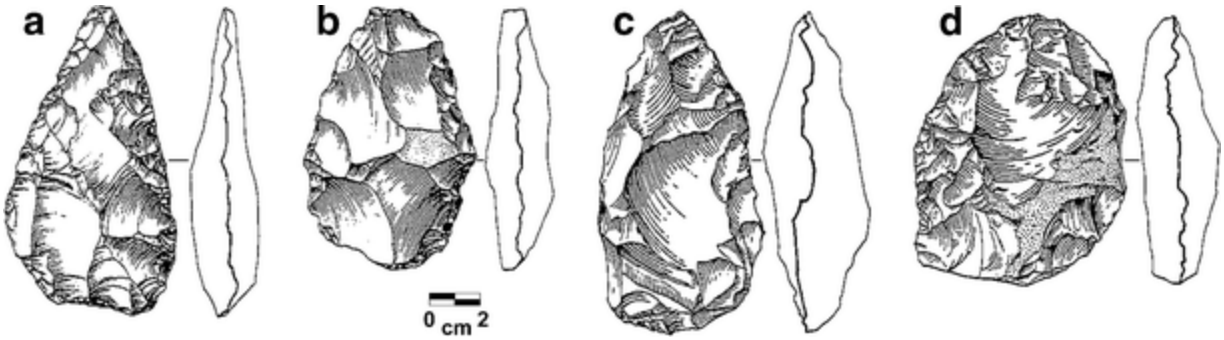

Fig. 23. Candidate handaxes as proposed by Becker (1971) from the sites of **a** Villestrup and **b** Fænø in Denmark. Late Neolithic/early Bronze Age preforms of bifacial tools from the workshop site of Fornæs (**c** and **d**). The latter were used by Glob (1972) to argue against the antiquity of the Danish handaxes

What, then, can be said of the human occupation of southern Scandinavia during the Eemian in particular and what, if anything, can it tell us about human adaptations? Sparse, but definitive, traces of human presence during the Eemian are recorded in Central Europe, although the northernmost site, Lehringen, is located approximately 400 km south of Hollerup. Eemian environments in Denmark appear, in general, to be very similar to nearby (and unquestionably occupied) areas. In terms of vegetation, Turner (2000, 222) observed that "[t]he most striking features of pollen diagrams from the Eemian is the strong parallelism in vegetation development right across Europe from the Massif Central, across the North European plain to Poland and beyond." This observation also applies to Denmark, which shows the general pattern of vegetation dominance and succession seen throughout most of northern Europe over the course of the Eemian: the initial spread of woodland and forest, mainly *Betula* (birch) and *Pinus* (pine), after the end of the Saalian, the appearance and expansion of temperate deciduous forests, mainly *Quercus* (oak) and *Corylus* (hazel), the arrival and rapid expansion of *Carpinus* (hornbeam), and, finally, the rise of boreal forests composed of *Betula*, *Pinus*, and *Picea* (spruce) just before the onset of the Weichselian (Björck et al. 2000; Gibbard and Glaister 2006)[3]. In terms of overall vegetation structure, therefore, sites such as Hollerup were broadly similar, though certainly not identical, to neighboring locales. For example, Scandinavia appears to have been beyond the northern limit of taxa such as *Abies* (silver birch), which, although cold-hardy, is sensitive to late spring frosts[4].

In regards to major climatic parameters, simulations based on general circulation models indicate that during the most temperate (and earliest) phase of the Eemian, central Jutland experienced slightly cooler summers, less severe winters, and lower precipitation than northern Germany, a pattern that largely mirrors modern gradients (Table 11). Paleobotanical indicators dating to the early Eemian suggest that central Jutland experienced minimum mean July temperatures approximately 1 °C lower than and minimum mean January temperatures about equal to those documented in the areas near Lehringen (Aalbersberg and Litt 1998). Although potentially important in terms of local ecology, these differences are much less pronounced than those seen

[3] In fact, this pattern differs little from the pollen zone scheme originally proposed by Jessen and Milthers (1928), which was based partly on Eemian-aged lacustrine deposits in Denmark.
[4] While *Abies* is present at Monmark in southern Denmark, Gibbard and Glaister (2006, 343, 346) argue against its autochthonous origin.

between northern Germany, which was within the Neandertal range, and areas further to the south (Aalbersberg and Litt, 1998). It therefore seems unlikely that these relatively minor dissimilarities played a significant role in limiting the expansion of Neandertals into Denmark. In fact, if they did indeed have trouble dealing with the dense interglacial forests of Central Europe, the more sparsely forested areas of southern Scandinavia may have offered them a cryptic northern refuge (cf. Stewart and Lister 2001).

Table 11. Modern and reconstructed Eemian climatic parameters for central Jutland and northern Germany

	Central Jutland		**Northern Germany**	
	Modern	**Eemian**	**Modern**	**Eemian**
Max. temperature, Aug. (°C)	18.9	21.4	22.0	23.6
Min. temperature, Aug. (°C)	12.1	13.2	11.6	12.7
Mean precipitation, Aug. (cm)	66.0	73.0	74.0	77.0
Max. temperature, Jan. (°C)	2.8	0.5	2.7	−0.4
Min. temperature, Jan. (°C)	−5.9	−0.4	−2.3	−9.0
Mean precipitation, Jan. (cm)	56.0	36.0	55.0	43.0

Modern and Eemian values were calculated in ArcGIS 10.0 using the spatial analyst tool and were based on the WorldClim monthly temperature and precipitation grids. Modern values are 1950–2000 averages (Hijmans et al., 2005), while the Eemian values are reconstructed for the very beginning of the interglacial period (Otto-Bliesner et al., 2006). Hollerup and Lehringen were used as the anchor points for central Jutland and northern Germany, respectively

One reason to suspect that the region was not favorable for human settlement, however, is the fact that mainland Denmark was isolated by a shallow waterway during parts of the Eemian (Larsen et al. 2009). In addition to the potential physical barrier to colonization, the effects of island insularity appear to have resulted in relatively low mammalian diversity. It is important to note that diversity during MIS 5e in Denmark is likely underestimated, as most species are represented by fewer than ten finds (Aaris-Sørensen et al. 1990, 27). Carnivore fossils in particular are completely absent from Eemian-aged deposits, the only evidence of their presence being the tooth marks identified by Møhl-Hansen (1955, 117) on one bone from Hollerup and the additional marks documented in this study. Nevertheless, the differences between the Danish record and the rich communities of Central Europe or even the somewhat less impoverished British Isles are striking (Table 12). Mammalian species diversity is known to correlate with population densities among modern hunter-gatherers and it is likely that the same relationship held for prehistoric hunter-gatherers (Morin 2008). So, one might argue that a peripheral geographic position, reduced faunal diversity, and partial isolation by water were sufficient to discourage human occupation of the region, as it apparently did for many other European mammals. A broadly analogous geographic and environmental situation can be found during MIS 5e on the British Isles, which itself was intermittently cut off from the European mainland, and arguments based mainly on geographic isolation and low human population densities in northwestern Europe have been made to explain the absence, or at least extreme scarcity, of Neandertals there (Ashton 2002; Ashton and Lewis 2002; Lewis et al. 2011). The analysis presented here thus supports the notion that large bodies of open water represented difficult if not insurmountable barriers to European Neandertals. While this does not contradict suggestions that movement *along* coastal areas was an important factor in the colonization of northern Europe by Neandertals—perhaps up to and including southern Scandinavia (Cohen et al. 2012)—it does imply that movement *across* attendant waterways was not a common occurrence.

Table 12. Mammalian faunal communities of northern Europe, the British Isles, and Denmark during MIS 5e

	Region		
	Northern Europe	**British Isles**	**Denmark**
Taxon			
LAGOMORPHA			
Lepus europaeus	X	0	0
L. timidus	0	X	0
RODENTIA			
Castor fiber	X	x	X
CARNIVORA			
Canis lupus	X	0	0
Crocuta crocuta	X	X	0
Felis lynx	X	0	0
F. sylvestris	X	X	0
Lutra lutra	X	0	0
Martes martes	X	0	0
Meles meles	X	X	0
Mustela purtorius	X	0	0
Panthera leo	X	X	0
P. pardus	X	0	0
Ursus arctos	X	X	0
Ursus spaleaus	X	0	0
Vulpes vulpes	X	X	0
PROBOSCIDEA			
Palaeoloxodon antiquus	X	X	X
PERISSODACTYLA			
Equus hydruntinus	X	0	0
Equus sp.	X	0	0
Stephanorhinus hemitoechus	X	X	0
Stephanorhinus kirchbergensis	X	0	X
ARTIODACTYLA			
Alces alces	X	0	0
Bison priscus	X	X	X
Bos primigenius	X	0	0
Capreolus capreolus	X	0	0
Cervus elaphus	X	X	X
Dama dama	X	X	X
Megaloceros giganteus	X	X	(X)
Sus scrofa	X	X	0
Hippopotamus amphibius	*	X	0
Bubalus murrensis	*	0	0
PRIMATES			
Homo sp.	X	0	0

Data from van Kolfschoten (2000), Currant and Jacobi (2001), and Aaris-Sørensen et al. (1990). X = presence; (X) = presence in secondary deposits presumed to derive from Eemian land surfaces; x = presence based on gnawed wood; * = absent from Central Europe but abundant in the Rhineland and regions to the west; 0 = absence.

The reanalysis of the Danish fallow deer material and weaknesses in the lithic evidence indicate that there is currently no solid support for a Neandertal occupation of the region. It is, however, important to reflect on how demographic, geological, taphonomic, and research-historical factors unique to Denmark may have biased or otherwise influenced its Paleolithic record. Because southern Scandinavia likely represented either a "zone of periodic extinction" or even a "zone of sterile invasion" (*sensu* Roebroeks, 2006, 429–430) far removed from Neandertal range center(s) within Europe, it is probable that, even if the region was inhabited, population densities would have been extremely low. Coupled with the fact that most Eemian-aged sites in nearby northern Europe sample low intensity occupations (Gaudzinski-Windheuser and Roebroeks, 2011), this means that any Neandertal traces in the region may be scarce even under the best of circumstances. While Eemian-aged geological localities are not a rarity in Denmark (see Fig. 3), it is also important to point out that none have yet been subjected to archaeological investigations. This is at least partly due to the traditional dominance of later prehistoric and medieval archaeology in Denmark. Therefore, very little systematic research in the country has been carried out with a mind towards the Paleolithic. What is more, many of the country's Eemian locales consist of shallow marine deposits rather than the sorts of depositional environments typically associated with human activities (e.g., lake margins). All of these factors should be seriously considered before a Neandertal presence in the region during the Eemian is rejected out of hand. Tantalizingly, some of the verified Middle Paleolithic finds from Germany mentioned above lie north of the Eemian waterway that separated Jutland from continental Europe (Fig. 3) and have tentatively been assigned a post-MIS 5e date (Hartz et al. 2012). While typological parallels can be misleading, the morphological similarities of the bifaces in these assemblages with those dated to MIS 3 in the British Isles (White and Pettitt 2011) may hint at a Neandertal occupation in the area after, rather than during, the Eemian.

Conclusions

The fallow deer assemblages from Hollerup have traditionally been interpreted as "uncontestable" (Holm, 1986, 76) evidence for the presence of humans in Scandinavia during the last interglacial. The taphonomic reanalysis of Hollerup and other Pleistocene fallow deer finds presented here calls this inference into question, as there is no definitive evidence that humans played any role whatsoever in the accumulation of the skeletons at any of the sites. Candidate Middle Paleolithic implements lack clear stratigraphic context and can potentially be confused with either geofacts or artifacts from later time periods. Therefore, there is at present no indication that Neandertals occupied southern Scandinavia during MIS 5e. A combination of latitude, an impoverished mammalian fauna, a wide (if relatively shallow) water body, and small source populations may have made the colonization of southern Scandinavia by Neandertals a difficult, and ultimately unsuccessful, venture. Future research aimed at the identification and systematic excavation of Eemian-aged deposits will reveal whether this conclusion needs revision. In addition, modeling-based approaches (Banks et al. 2006, 2008) may assist in better delimiting Neandertal niche space during, as well as before and after, MIS 5e, and large-scale survey projects to the west of the maximal Weichselian glacial advance (like those recently conducted with success in the Netherlands; Niekus et al. 2011) may ultimately produce new empirical evidence that will allow the question of Neandertal presence in Denmark to be resolved.

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References

Aalbersberg G, Litt T (1998) Multiproxy climate reconstructions for the Eemian and early Weichselian. J Quat Sci 13:367–390

Aaris-Sørensen K (2009) Diversity and dynamics of the mammalian fauna in Denmark throughout the last glacial–interglacial cycle, 115–0 kyr BP. Fossils Strata 57:1–59

Aaris-Sørensen K, Petersen KS, Tauber H (1990) Danish finds of mammoth (*Mammuthus primigenius* (Blumenbach)). Stratigraphical position, dating and evidence of Late Pleistocene environment. Dan Geol Unders B 14:1–44

Andersen ST (1966) Interglacial vegetational succession and lake development in Denmark. Paleobotanist 15:117–127

Andrews P (1990) Owls, caves and fossils. University of Chicago Press, Chicago

Ashton NM (2002) Absence of humans in Britain during the last interglacial (Oxygen Isotope Stage 5e). In: Tuffreau A, Roebroeks W (eds) Le Dernier Interglaciaire et les Occupations Humaines du Paléolithique Moyen. Centre d'études et de recherches préhistoriques, Lille, pp 93–103

Ashton NM, Lewis SG (2002) Deserted Britain: declining populations in the British late Middle Pleistocene. Antiquity 76:388–396

Baales M, Jöris O, Justus A, Roebroeks W (2000) Natur oder Kultur? Zur Frage ältestpaläolithischer Artefaktensembles aus Hauptterrassenschottern in Deutschland. Germania 78:1–20

Banks WE, d'Errico F, Dibble HL, Krishtalka L, West D, Olszewski DI, Peterson AT, Anderson DG, Gilliam JC, Montet-White A, Crucifix M, Marean CW, Sánchez-Goñi M-F, Wohlfarth B, Vanhaeran M (2006) Eco-cultural niche modeling: new tools for reconstructing the geography and ecology of past human populations. PaleoAnthropology 2006:68–83

Banks WE, D'Errico F, Peterson AT, Kageyama M, Sima A, Sánchez-Goñi M-F (2008) Neanderthal extinction by competitive exclusion. PLoS One 3:e3972

Becker CJ (1971) Istidsmandens Redskaber. Skalk 4:3–7

Behrensmeyer AK (1978) Taphonomic and ecologic information from bone weathering. Paleobiology 4:150–162

Behrensmeyer AK (1987) Taphonomy and hunting. In: Nitecki MH, Nitecki DV (eds) The evolution of human hunting. Plenum, New York, pp 432–450

Behrensmeyer AK, Gordon KD, Yanagi GT (1986) Trampling as a cause of bone surface damage and pseudo-cutmarks. Nature 319:768–771

Berthelsen W (1944) Stenalderbopladser i Sønderkjær og Vejledalen: Bidrag til Kendskabet til den mesolitiske Kulturperiode i Sydøstjylland. Munksgaard, København

Björck S, Noe-Nygaard N, Wolin J, Houmark-Nielsen M, Hansen HJ, Snowball I (2000) Eemian lake development, hydrology and climate: a multi-stratigraphic study of the Hollerup site in Denmark. Quat Sci Rev 19:509–536

Bjørn A (1928) Nogen norkse stenalderproblemer. Nor Geol Tidsskr 10:53–75

Blasco R, Fernández Peris J (2012) A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). Quat Int 252:16–31

Blumenschine RJ (1986) Carcass consumption sequences and the archaeological distinction of scavenging and hunting. J Hum Evol 15:639–659

Blumenschine RJ, Marean CW, Capaldo SD (1996) Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. J Archaeol Sci 23:493–507

Bologna P, Di Stefano G, Manzi G, Petronio C, Sardella R, Squazzini E (1994) Late Pleistocene mammals from Melpignano (LE) "Ventarole": preliminary analysis and correlation. Boll Soc Paleontol Ital 33:265–274

Brain CK (1974) Some suggested procedures in the analysis of bone accumulations from southern African Quaternary sites. Ann Transvaal Mus 29:1–8

Brauer A, Allen JRM, Mingram J, Dulski P, Wulf S, Huntley B (2007) Evidence for last interglacial chronology and environmental change from Southern Europe. Proc Natl Acad Sci 104:450–455

Braun A, Pfeiffer T (2002) Cyanobacterial blooms as the cause of a Pleistocene large mammal assemblage. Paleobiology 28:139–154

Brinch Petersen E (2009) The human settlement of southern Scandinavia 12500–8700 cal BC. In: Street M, Barton RNE, Terberger T (eds) Humans, environment and chronology of the late glacial of the North European Plain. Verlag des Römisch-Germanischen Zentralmuseums, Mainz, pp 89–129

Brown WAB, Chapman NG (1990) The dentition of fallow deer (*Dama dama*): a scoring scheme to assess age from wear of the permanent molariform teeth. J Zool 221:659–682

Bunn HT (1981) Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. Nature 291:574–577

Bunn HT (1982) Meat-eating and human evolution: studies on the diet and subsistence patterns of Plio-Pleistocene hominids in East Africa. Dissertation, University of California, Berkeley

Bunn HT (1986) Patterns of skeletal part representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. J Hum Evol 15:673–690

Bunn HT (2001) Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene *Homo*. In: Stanford CB, Bunn HT (eds) Meat-eating and human evolution. Oxford University Press, Oxford, pp 199–218

Capaldo SD (1997) Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. J Hum Evol 33:555–597

Capaldo SD, Blumenschine RJ (1994) A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing in bovid long bones. Am Antiq 59:724–748

Capaldo SD, Peters CR (1995) Skeltal inventories from wildebeest drownings at lakes Masek and Ndutu in the Serengetic ecosystem of Tanzania. J Archaeol Sci 22:385–408

Chapman DI, Chapman NG (1970) Development of the teeth and mandibles of fallow deer. Acta Theriol XV:111–131

Chapman DI, Chapman NG (1975) Fallow deer: their history, distribution and biology. Terence Dalton Limited, Suffolk

Cohen KM, MacDonald K, Joordens JCA, Roebroeks W, Gibbard PL (2012) The earliest occupation of north-west Europe: a coastal perspective. Quat Int 271:70–83

Currant A, Jacobi R (2001) A formal mammalian biostratigraphy for the Late Pleistocene of Britain. Quat Sci Rev 20:1707–1716

Dart RA (1957) The Osteodontokeratic culture of *Australopithecus prometheus*. Transvaal Museum, Pretoria

Daujeard C, Fernandes P, Guadelli J-L, Monchel H-M, Santagata C, Raynal J-P (2012) Neanderthal subsistence strategies in Southeastern France between the plains of the Rhone Valley and the mid-mountains of the Massif Central (MIS 7 to MIS 3). Quat Int 252:32–47

Dennell RW, Martinón-Torres M, Bermúdez de Castro JM (2011) Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. Quat Sci Rev 30:1511–1524

Domínguez-Rodrigo M (1997) Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge (Tanzania): an experimental approach using cutmark data. J Hum Evol 33:669–690

Domínguez-Rodrigo M, Piqueras A (2003) The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviors. J Archaeol Sci 30:1385–1391

Domínguez-Rodrigo M, de Juana S, Galán AB, Rodríguez M (2009) A new protocol to differentiate trampling marks from butchery cut marks. J Archaeol Sci 36:2643–2654

Domínguez-Rodrigo M, Pickering TR, Bunn HT (2010) Configurational approach to identifying the earliest hominin butchers. Proc Natl Acad Sci 107:20929–20934

Donner J (1995) The quaternary history of Scandinavia. Cambridge University Press, Cambridge

Faith JT (2007) Sources of variation in carnivore tooth-mark frequencies in a modern spotted hyena (*Crocuta crocuta*) den assemblage, Amboseli Park, Kenya. J Archaeol Sci 34:1601–1609

Faith JT, Behrensmeyer AK (2006) Changing patterns of carnivore modification in a landscape bone assemblage, Amboseli Park, Kenya. J Archaeol Sci 33:1718–1733

Faith JT, Marean CW, Behrensmeyer AK (2007) Carnivore competition, bone destruction, and bone density. J Archaeol Sci 34:2025–2034

Faux CM, Padian K (2007) The opisthotonic posture of vertebrate skeletons: postmortem contraction or death throes? Paleobiology 33:201–226

Finlayson JC (2004) Neanderthals and modern humans: an ecological and evolutionary perspective. Cambridge University Press, Cambridge

Fiorillo A (1989) An experimental study of trampling: implications for the fossil record. In: Bonnichsen R, Sorg MH (eds) Bone modification. Center for the Study of the First Americans, Orono, pp 61–71

Galán AB, Rodríguez M, de Juana S, Domínguez-Rodrigo M (2009) A new experimental study on percussion marks and notches and their bearing on the interpretation of hammerstone-broken faunal assemblages. J Archaeol Sci 36:776–784

Gamble C (1987) Man the shoveller: alternative models for Middle Pleistocene colonization and occupation in northern latitudes. In: Soffer O (ed) The Pleistocene old world: regional perspectives. Plenum, New York, pp 81–98

Gaudzinski S (2004) A matter of high resolution? The Eemian interglacial (OIS 5e) in north-central Europe and Middle Palaeolithic subsistence. Int J Osteoarchaeol 14:201–211

Gaudzinski-Windheuser S, Roebroeks W (2011) On Neanderthal subsistence in last interglacial forested environments in northern Europe. In: Conard NJ, Richter J, Condemi S (eds) Neanderthal lifeways, subsistence and technology: one hundred fifty years of Neanderthal study. Springer, New York, pp 61–71

Gibbard PL, Glaister C (2006) Pollen stratigraphy of the Late Pleistocene sediments at Mommark, Als, South Denmark. Boreas 35:332–348

Gifford DP (1981) Taphonomy and paleoecology: a critical review of archaeology's sister disciplines. Adv Archaeol Method Theory 14:365–437

Glob PV (1963) Arkæologiens flyvende tallerkener. Danmarks rigdom på flint vildleder amatørarkæologerne. Berlingske Tidende, October 27, 1963,

Glob PV (1972) Farlig flint. Skalk 1:18–20

Guadelli J-L (2008) La gélifraction des restes fauniques. Expérimentation et transfert au fossile. Annales de Paléontologie 94:121–165

Hachmann R (1974) Rezension: A. Rust, Werkzeuge des Frühmenschen in Europa. Hist Z 217:644

Hartz N (1909) Bidrag til Danmarks tertiære og diluviale flora. Danmarks Geologiske Undersøgelse II 22:1–292

Hartz S (1986) Paläolitische Funde aus dem Altmoränengebiet Nordfrieslands. Offa 43:105–147

Hartz S, Fiedler L (1997) Älteres Paläolithikum aus dem Gebiet nördlich der Elbe. In: Fiedler L (ed) Archäologie der ältesten Kultur in Deutschland Ein Sammelwerk zum älteren Paläolithikum der Zeit des *Homo erectus* und des frühen Neandertalers. Landesamt für Denkmalpflege Hessen, Wiesbaden, pp 356–363

Hartz N, Østrup E (1899) Danske Diatomejordaflejnnger og deres Diatoméer. Danmarks Geologiske Undersøgelse II 9:1–80

Hartz S, Beuker JR, Niekus MJLT (2012) Neanderthal finds in Schleswig Holstein?—Middle Palaeolithic flintscatters in Northern Germany. In: Niekus MJLT, Barton RNE, Street M, Terberger T (eds) A mind set on flint: studies in honour of Dick Stapert. Barkhuis, Groningen, pp 93–106

Haynes G (1983) Frequencies of spiral and green-bone fractures on ungulate limb bones in modern surface assemblages. Am Antiq 48:102–114

Haynes G (1988) Mass deaths and serial predation: comparative taphonomic studies of modern large mammal death sites. J Archaeol Sci 15:219–235

Heimdahl J (2006) Spår av en mellanpaleolitisk befolkning i Sverige? Fornvännen 101:1–8

Hijma MP, Cohen KM, Roebroeks W, Westerhoff WE, Busschers FS (2012) Pleistocene Rhine–Thames landscapes: geological background for hominin occupation of the southern North Sea region. J Quat Sci 27:17–39

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Højrup O (1947) Bopladser med håndkiler fra Roskilde fjord. Aarbøger for nordisk Oldkyndighed og Historie 1946:95–102

Holm J (1986) The Quaternary and the Early/Middle Palaeolithic of Denmark. In: Tuffreau A, Sommé J (eds) Chronostratigraphie et faciès culturels du Paléolithique inferiéur et moyen dans l´Europe du Nord-Ouest. Supplément au Bulletin de l'Association Francaise pour l'Étude du Quaternaire, Paris, pp 75–80

Holm J, Larsson L (1995) The earliest occupation of Europe: Scandinavia. In: Roebroeks W, von Kolfschoten T (eds) The earliest occupation of Europe. Leiden University, Leiden, pp 193–205

Hosfield R (2011) The British Lower Palaeolithic of the early Middle Pleistocene. Quat Sci Rev 30:1486–1510

Houmark-Nielsen M (1987) Pleistocene stratigraphy and glacial history of the central part of Denmark. Bull Geol Soc Den 36:1–189

Hublin J-J, Roebroeks W (2009) Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments. Comptes Rendus Palevol 8:503–509

Hutson JM (2012) Neotaphonomic measures of carnivore serial predation at Ngamo Pan as an analog for interpreting open-air faunal assemblages. J Archaeol Sci 39:440–457

Israelson C, Björck S, Hawkesworth CJ, Noe-Nygaard N (1998) Uranium-series isotopes from Eemian lake deposits, Hollerup, Denmark. Bull Geol Soc Den 44:173–179

Jensen JV (1910) Dansk Natur. Riget 1:1–12

Jessen K, Milthers V (1928) Interglacial fresh-water deposits in Jutland and Northwest Germany. Danmarks Geologiske Undersøgelse II 48:1–379

Johansen L, Stapert D (1996) Handaxes from Denmark: Neandertal tools or 'vicious flints'? Palaeohistoria 37(38):1–28

Johnson E (1985) Current developments in bone technology. Adv Archaeol Method Theory 8:157–235

Karr LP, Outram AK (2012) Tracking changes in bone fracture morphology over time: environment, taphonomy, and the archaeological record. J Archaeol Sci 39:555–559

Kindler L, Gaudzinski-Windheuser S, Roebroeks W, Brühl E, De Loecker D, Jagich A, Laurat T (2010) Neumark-Nord: Neandertaler an den Ufern des Geiseltalsees. Archäologie in Deutschland 2:6–11

Kjærgaard PC (2013) Inventing *Homo gardarensis*: Prestige, pressure and human evolution in interwar Scandinavia. Science in Context (in press).

Krause J, Orlando L, Serre D, Viola B, Prüfer K, Richards MP, Hublin J-J, Hänni C, Derevianko AP, Pääbo S (2007) Neanderthals in central Asia and Siberia. Nature 449:902–904

Kronborg C (1983) Glacialstratigrafien i Øst-og Midtjylland. Dissertation, Aarhus Universitet, Aarhus

Kronborg C, Mejdahl V (1989) Thermoluminescence dating of Eemian and early Weichselian deposits in Denmark. Quat Int 3/4:93–99

Kronborg C, Bender H, Bjerre R, Friborg R, Jacobsen HO, Kristiansen L, Rasmussen P, Sørensen PR, Larsen G (1990) Glacial stratigraphy of East and Central Jutland. Boreas 19:273–287

Larsen NK, Knudsen KL, Krohn CF, Kronborg C, Murray AS, Nielsen OB (2009) Late Quaternary ice sheet, lake and sea history of southwest Scandinavia—a synthesis. Boreas 38:732–761

Lewis SG, Ashton NM, Jacobi R (2011) Testing human presence during the late interglacial (MIS 5e): a review of the British evidence. In: Ashton NM, Lewis SG, Stringer CB (eds) The ancient human occupation of Britain. Elsevier, New York, pp 125–164

Lyman RL (1994) Vertebrate taphonomy. Cambridge University Press, Cambridge

Mania D (ed) (2010) Neumark-Nord: ein interglaziales Ökosystem des mittelpaläolithischen Menschen, vol 62. Veröffentlichungen des Landesamtes für Archäologie Sachsen Anhalt, Halle

Mania D, Thomae M, Litt T, Weber T (1990) Neumark-Gröbern: Beiträge zur Jagd des mittelpaläolithischen Menschen. Deutscher Verlag der Wissenschaften, Berlin

Marean CW (1991) Measuring the post-depositional destruction of bone in archaeological assemblages. J Archaeol Sci 18:677–694

Marean CW, Kim SY (1998) Mousterian large-mammal remains from Kobeh Cave: behavioral implications for Neanderthals and early modern humans. Curr Anthropol 39:S79–S113

Marean CW, Abe Y, Frey CJ, Randall RC (2000) Zooarchaeological and taphonomic analysis of the Die Kelders Cave 1 Layers 10 and 11 Middle Stone Age larger mammal fauna. J Hum Evol 38:197–233

Marean CW, Domínguez-Rodrigo M, Pickering TR (2004) Skeletal element equifinality in zooarchaeology begins with method: the evolution and status of the “shaft critique”. J Taphon 2:69–98

Mathiassen T (1935) Primitive flintredskaber fra Samsø. Aarbøger for nordisk Oldkyndighed og Historie 1934:39–54

McElligott AG, Hayden TJ (2000) Lifetime mating success, sexual selection and life history of fallow bucks (*Dama dama*). Behav Ecol Sociobiol 48:203–210

McElligott AG, Altwegg R, Hayden TJ (2002) Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). Proc R Soc Lond Ser B-Biol Sci 269:1129–1137

Mejdahl V, Funder S (1994) Luminescence dating of Late Quaternary sediments from East Greenland. Boreas 23:525–535

Meller H (ed) (2010) Elefantenreich: eine Fossilwelt in Europa. Landesamt für Vorgeschichte, Halle

Miracle P (2005) Late Mousterian subsistence and cave use in Dalmatia: the zooarchaeology of Mujina Pecina, Croatia. Int J Osteoarchaeol 15:84–105

Møhl-Hansen U (1955) Første sikre spor af mennesker fra interglacialtid i Denmark. Marvspaltede knogler fra diatoméjorden ved Hollerup. Aarbøger for nordisk Oldkyndighed og Historie 1954:101–126

Montelius GOA (1921) Palaeolithic implements found in Sweden. Antiqu J 1:98–104

Moore NP, Cahill JP, Kelly PF, Hayden TJ (1995) An assessment of five methods of age determination in an enclosed population of fallow deer (*Dama dama*). Proc R Ir Acad 95B:27–34

Morin E (2008) Evidence for declines in human population densities during the early Upper Paleolithic in western Europe. Proc Natl Acad Sci 105:48–53

Morlan RE (1984) Toward the definition of criteria for the recognition of artificial bone alteration. Quat Res 22:160–171

Mortensen MF, Holm J, Christensen C, Aaris-Sørensen K (2009) De første mennesker i Danmark. Nationalmuseets Arbejdsmark 2008:69–82

Niekus MJLT, Stapert D, Beuker JR, Johansen L (2011) A new site of the Mousterian of Acheulian Tradition in the northern Netherlands. Quartär 58:67–92

Niven LB, Steele TE, Rendu W, Mallye J-B, McPherron SP, Soressi M, Jaubert J, Hublin J-J (2012) Neandertal mobility and large-game hunting: the exploitation of reindeer during the Quina Mousterian at Chez-Pinaud Jonzac (Charente-Maritime, France). J Hum Evol 63:624–635

Noe-Nygaard N (1977) Butchering and marrow fracturing as a taphonomic factor in archaeological deposits. Paleobiology 3:218–237

Otto-Bliesner BL, Marshall SJ, Overpeck JT, MIller GH, Hu A, CAPE Last Interglacial Project members (2006) Simulating arctic climate warmth and icefield retreat in the last interglaciation. Science 311:1751–1753

Pei WC (1938) Le rôle des animaux et des causes naturelles dans le cassure des os. Geological Survey of China, Peiping

Petersen PV (2008) Flint fra Danmarks oldtid. Museerne.dk, København

Pettitt PB, Niskanen M (2005) Neanderthals in Susiluola Cave, Finland, during the last interglacial period? Fennoscandia archaeologica XXII:79–87

Pfeiffer T (1995) Das Vorkommen von *Dama dama* in Mitteleuropa im Pleistozän unter besonderer Berücksichtigung der Funde von Neumark-Nord (Sachsen Anhalt). Z Jagdwiss 41:157–170

Pfeiffer T (1999) Die Stellung von *Dama* (Cervidae, Mammalia) im System plesiometacarpaler Hirsche des Pleistozän. Courier Forschungsinstitut Senckenberg 211:1–218

Pickering TR, Egeland CP (2006) Experimental patterns of hammerstone percussion damage on bones and zooarchaeological inferences of carcass processing intensity by humans. J Archaeol Sci 33:459–469

Pickering TR, Marean CW, Domínguez-Rodrigo M (2003) Importance of limb bone shaft fragments in zooarchaeology: a response to “On in situ attrition and vertebrate body part profiles” (2002) by M.C. Stiner. J Archaeol Sci 30:1469–1482

Pobiner BL, Blumenschine RJ (2003) A taphonomic perspective on Oldowan hominid encroachment on the carnivoran paleoguild. J Taphon 1:115–141

Prufer OH (1956) Review of: Artefakte aus der Zeit des Homo heidelbergensis in Süd- und Norddeutschland. Proc Prehistoric Soc 22:218–219

Riede F (2009) Climate change, demography and social relations: an alternative view of the Late Palaeolithic pioneer colonization of southern Scandinavia. In: McCartan S, Schulting R, Warren G, Woodman P (eds) Mesolithic horizons: papers presented at the Seventh International Conference on the Mesolithic in Europe, Belfast 2005. Oxbow Books, Oxford, pp 3–10

Roebroeks W (2006) The human colonisation of Europe: where are we? J Quat Sci 21:425–435

Roebroeks W, Speelers B (2002) Last interglacial (Eemian) occupation of the North European Plain and adjacent areas. In: Tuffreau A, Roebroeks W (eds) Le Dernier Interglaciaire et les Occupations Humaines du Paléolithique Moyen. Centre d’études et de recherches préhistoriques, Lille, pp 31–39

Roebroeks W, Conard NJ, van Kolfschoten T (1992) Dense forests, cold steppes, and the Palaeolithic settlement of northern Europe. Curr Anthropol 33(5):551–586

Roebroeks W, Hublin J-J, MacDonald K (2011) Continuities and discontinuities in Neandertal presence: a closer look at northwestern Europe. In: Ashton NM, Lewis S, Stringer CB (eds) The ancient human occupation of Britain. Elsevier, Amsterdam, pp 113–124

Schüler T (2010) ESR-Datierung von Zahnschmelzproben der archäologischen Fundhorizonte von Neumark-Nord. In: Meller H (ed) Elefantenreich: eine Fossilwelt in Europa. Landesamt für Vorgeschichte, Halle, pp 71–75

Schultz H-P (2002) The lithic industry from layers IV-V, Susiluola Cave, western Finland, dated to the Eemian interglacial. Préhistoire Européenne 16–17:43–56

Schultz H-P (2007) Artefact-geofact analysis of the lithic material from the Susiluola Cave. Fennoscandia archaeologica XXIV:64–75

Schultz H-P (2010) The Susiloula Cave site in western Finland—evidence of the northernmost Middle Palaeolithic settlement in Europe. In: Burdukiewicz JM, Wisniewski A (eds) Middle Palaeolithic human activity and palaeoecology: new discoveries and ideas. Wydawnictwo Uniwersytetu Wroclawskiego, Wroclaw, pp 47–67

Schultz H-P, Eriksson B, Hirvas H, Huhta P, Jungner H, Purhonen P, Ukkonen P, Rankama T (2002) Excavations at Susiluola Cave. Suomen Museo 2002:5–45

Schwabedissen H (1968) Archaische Züge im Meso- und Neolithikum des Nordens. In: Piveteau J (ed) La Préhistoire, Problèmes et Tendances. Editions du CNRS, Paris, pp 369–382

Schwabedissen H (1970) Zur verbreitung der Faustkeile in Mitteleuropa. In: Gripp K, Schüttrumpf R, Schwabedissen H (eds) Frühe Menschheit und Umwelt I (Festschrift Alfred Rust). Böhlau, Köln and Graz, pp 61–98

Selva N, Jedrzejewska B, Jedrzejewski W, Wajrak A (2003) Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). Ecoscience 10:303–311

Shipman P (1981) Life history of a fossil: an introduction to taphonomy and paleoecology. Harvard University Press, Cambridge

Shipman P, Rose J (1988) Bone tools: an experimental approach. In: Olsen SL (ed) Scanning electron microscopy in archaeology. British Archaeological Reports 452, Oxford, pp 303–335

Slimak L, Svendsen JI, Mangerud J, Plisson H, Heggen HP, Brugère A, Pavlov PY (2011) Late Mousterian persistence near the Arctic Circle. Science 332:841–845

Slimak L, Svendsen JI, Mangerud J, Plisson H, Heggen HP, Brugère A, Pavlov PY (2012) Response to "Comment on Late Mousterian persistence near the Arctic Circle". Science 335:167b

Steele TE (2005) Comparing methods for analysing mortality profiles in zooarchaeological and palaeontological samples. Int J Osteoarchaeol 15:404–420

Steensby HP (1908) Racestudier i Danmark. Geografisk Tidsskrift 19:135–145

Steensby HP (1911) Foreløbige Betragtninger over Danmarks Raceantropologi. Meddelelser om Danmarks Antropologi 1:83–148

Stewart JR (2005) The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3. Quat Int 137:35–46

Stewart JR, Lister AM (2001) Cryptic northern refugia and the origins of the modern biota. Trends Ecol Evol 16:608–613

Stiner MC, Munro ND, Sanz M (2012) Carcass damage and digested bone from mountain lions (*Felis concolor*): implications for carcass persistence on landscapes as a function of prey age. J Archaeol Sci 39:896–907

Stringer CB, Hublin J-J (1999) New age estimates for the Swanscombe hominid, and their significance for human evolution. J Hum Evol 37:873–877

Stringer CB, Finlayson JC, Barton RNE, Fernández-Jalvo Y, Cáceres I, Sabin RC, Rhodes EJ, Currant AP, Rodríguez-Vidal J, Giles-Pacheco F, Riquelme-Cantal JA (2008) Neanderthal exploitation of marine mammals in Gibraltar. Proc Natl Acad Sci 105:14319–14324

Thompson JC (2005) The impact of post-depostional processes on bone surface modification frequencies: a corrective strategy and its application to the Loiyangalani Site, Serengeti Plain, Tanzania. J Taphon 3:67–90

Todd LC (1987) Taphonomy of the Horner II bonebed. In: Frison GC, Todd LC (eds) The Horner Site: the type site of the Cody Cultural Complex. Academic Press, Orlando, pp 107–198

Troels-Smith J (1995) Claudi-kiler, østersbanker og tidevand. In: Hansen HH, Aaby B (eds) Stavns Fjord: et natur- og kulturhistorisk forskningsområde på Samsø. Nationalmuseet, København, pp 59–67

Turner C (2000) The Eemian interglacial in the North European plain and adjacent areas. Geol Mijnb 79:217–231

Valensi P (2000) The archaeozoology of Lazaret Cave (Nice, France). Int J Osteoarchaeol 10:357–367

Valensi P, Crégut-Bonnoure E, Defleur A (2012) Archaeozoological data from the Mousterian level from Moula-Guercy (Ardèche, France) bearing cannibalised Neanderthal remains. Quat Int 252:48–55

van Andel TH, Davies W (eds) (2003) Neanderthals and modern humans in the European landscape during the last glaciation. McDonald Institute for Archaeological Research, Cambridge

van Kolfschoten T (2000) The Eemian mammal fauna of central Europe. Geologie en Mijnbouw 79:269–281

Villa P, Mahieu E (1991) Breakage patterns of human long bones. J Hum Evol 21:27–48

von den Driesch A (1976) A guide to the measurement of animal bones from archaeological sites. Peabody Museum of Archaeology and Ethnology, Cambridge

White M, Pettitt P (2011) The British Late Middle Palaeolithic: an interpretative synthesis of Neanderthal occupation at the northwestern edge of the Pleistocene world. J World Preh 24:25–97

Zwyns N, Roebroeks W, McPherron SP, Jagich A, Hublin J-J (2012) Comment on “Late Mousterian persistence near the Arctic Circle”. Science 335:167c

Appendix

Table 13. Osteometric data (measures in millimeters) from Danish assemblages

Element (Find)	GLP	GB	LG	GB	Bd	BT	Bp	BFd	BFp	BPC	LO	DPA	Ddl	Ddm	GL	Dm	GLm	GLl	Dl	GLpe
Scapula																				
Find V	43.46	–	33.06	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Find V	43.40	–	33.62	29.24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Humerus																				
Find I	–	–	–	–	44.47	37.79	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Find V	–	–	–	–	42.31	–	50.99	–	–	–	–	–	–	–	–	–	–	–	–	–
Find V	–	–	–	–	42.39	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Radius																				
Find V	–	–	–	–	–	–	40.22	34.00	36.29	–	–	–	–	–	–	–	–	–	–	–
Find V	–	–	–	–	–	–	–	33.94	–	–	–	–	–	–	–	–	–	–	–	–
Ulna																				
Find V	–	–	–	–	–	–	–	–	–	20.33	–	–	–	–	–	–	–	–	–	–
Find V	–	–	–	–	–	–	–	–	–	–	51.72	35.07	–	–	–	–	–	–	–	–
Fused 2 + 3 carpal																				
Find V	–	19.50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Metacarpal																				
Find V	–	–	–	–	29.30	–	28.51	–	–	–	–	–	19.83	19.71	209.16	–	–	–	–	–
Find VI	–	–	–	–	32.50	–	–	–	–	–	–	–	22.29	21.72	–	–	–	–	–	–
Find VI	–	–	–	–	32.51	–	32.03	–	–	–	–	–	22.34	21.75	229.23	–	–	–	–	–
Tibia																				
Find V	–	–	–	–	35.46	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Find VI	–	–	–	–	38.11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Find IX	–	–	–	–	33.93	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Find XI					37.93															
Find XIV	–	–	–	–	39.02		–	–	–	–	–	–	–	–	–	–	–	–	–	–
Astragalus																				
Find VI	–	–	–	–	28.21	–	–	–	–	–	–	–	–	–	–	25.43	41.78	42.87	23.85	–
Find IX	–	–	–	–	24.59	–	–	–	–	–	–	–	–	–	–	22.66	37.08	37.54	20.60	–
Fused central + 4 tarsal																				
Find VI	–	34.89	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Find IX	–	31.50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Element (Find)	GLP	GB	LG	GB	Bd	BT	Bp	BFd	BFp	BPC	LO	DPA	Ddl	Ddm	GL	Dm	GLm	GLl	Dl	GLpe
Metatarsal																				
Find V	–	–	–	–	31.30	–	–	–	–	–	–	–	20.86	20.51	–	–	–	–	–	–
Find V	–	–	–	–	31.06	–	27.40	–	–	–	–	–	20.73	20.41	–	–	–	–	–	–
Find VI	–	–	–	–	34.54	–	–	–	–	–	–	–	22.72	22.46	–	–	–	–	–	–
Phalanx I																				
Find V	–	–	–	–	13.36	–	14.72	–	–	–	–	–	–	–	–	–	–	–	–	42.71
Find V	–	–	–	–	13.42	–	14.65	–	–	–	–	–	22.29	21.72	–	–	–	–	–	43.11
Phalanx II																				
Find V	–	–	–	–	11.88	–	14.16	–	–	–	–	–	–	–	18.81	–	–	–	–	28.37
Find V	–	–	–	–	–	–	14.07	–	–	–	–	–	–	–	–	–	–	–	–	–

Measurements after von den Driesch (1976)